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GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

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HYBRID VIGOR IN EGG-PLANTS AND ITS PRACTICAL UTILIZATION[1]

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Received October 11, 1929

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The egg-plant, *Solanum Melongena*, L., is one of the most important vegetable crops in Japan, its fruit being used in various ways for cooking and pickling. Seed is readily produced by artificial crossing and a small amount can be used for a comparatively large area. Hence, if this plant exhibits hybrid vigor in an appreciable degree, first generation hybrids may be utilized for commercial culture. With this in view, the author made an experiment with forty-one intervarietal crosses of egg-plants, comparing them with their parental strains, during four years from 1922 till 1925. The present paper reports the results and the extent of the practical utilization of F_1 crosses of this plant.

[1] Contribution No. 13 of the Department of Horticulture of the SAITAMA AGRICULTURAL EXPERIMENT STATION. A part of this paper has been formerly published in Japanese in *Agriculture and Horticulture*, Tokyo, Vol. 3, 1928.

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MATERIAL AND GENERAL METHODS

Artificial crosses shown in table 1 were made among varieties which were assembled from various regions of Japan. The parental seed for comparison was raised from the same plant used for each cross, except with a few varieties which were selfed for three or four generations before crossing and were judged to be pure lines. Moreover, all the parental seeds were produced by artificial self-fertilization, for, as the author (1924, 1926) has already reported, the egg-plant is sometimes naturally crossed to an appreciable degree although ordinarily it is naturally self-fertilized.

The hybrid and their parental strains were grown, as a matter of course, under as uniform conditions as possible. The seedlings were raised in a hot bed and replanted in the field in one meter rows fifty centimeters apart.

THE IMMEDIATE EFFECT OF CROSS-POLLINATION ON THE SIZE OF SEED

Experimental result

Table 2 shows the weight of one thousand grains each of the F_1 seed and the selfed seed of their parental plants. There are only 28 combinations instead of 41, for such combinations were omitted from the study where either the crossed or the selfed fruit rotted before perfect maturity. From the table we can see that, in comparison with the selfed seed of the mother parent, most crosses are heavier. There are 5 crosses lighter, 1 same and 22 heavier, and in the average of all the crossed seed exceeds the selfed seed by 18.3 percent. The decrease in weight of the five lighter crosses is 9 percent or less. The amount of increase shows a wide variation as given in table 3, and the highest increase is 71 percent in No. 20.

There are 6 crosses in which the F_1 seed is heavier than the seed of either parent. Although, in some of these crosses, the increase is slight and can not be regarded as significant, No. 20 shows an increase of 59 percent over the heavier parent.

To see whether or not the size of seed of the pollen parent has any effect on that of the F_1 seed, let us examine the relation between the difference in grams of the pollen parent from the mother parent and the percentage of increase or decrease of the F_1 as compared with the mother parent. We can pick up some cases that appear to show a close relation, such as +2.00 grams and +71 percent in No. 6, +1.89 grams and +52 percent in No. 4, and −1.54 grams and −7 percent in No. 22. On the other hand, however, there are several crosses in which we can not see any effect of the size of seed of the pollen parent, the most conspicuous

TABLE 1

Combinations of the crosses studied with the year the F_1 was grown.

CROSS NO.	NAME OF VARIETY		YEAR GROWN
	MOTHER PARENT	POLLEN PARENT	
1	Sironasu	Okute Yamanasu	1922
2	Kawabe Naganasu	Okute Yamanasu	"
3	Kawabe Naganasu	Turuboso Sennari	"
4	Sironasu	Sinkuro	1923
5	Kintyaku	Sinkuro	"
6	Kawabe Naganasu	Sinkuro	"
7	Minden	Sinkuro	"
8	Yuiki Yamanasu	Sinkuro	"
9	Daien	Sinkuro	"
10	Wase Marunasu	Sinkuro	"
11	Turuboso Sennari	Okute Yamanasu	"
12	Wase Marunasu	Okute Yamanasu	"
13	Wase Sennari	Okute Yamanasu	"
14	Okute Yamanasu	Aizu Tukenasu	"
15	Kintyaku	Turuboso Sennari	"
16	Minden	Sironasu	"
17	Wase Hetamurasaki	Wase Sennari	"
18	Aizu Tukenasu	Sinkuro	"
19	Sironasu	Kintyaku	1924
20	Sironasu	Tsiba Wase	"
21	Sironasu	Aizu Sinkuro	"
22	Kintyaku	Tiba Wase	"
23	Kintyaku	Aizu Sinkuro	"
24	Sinkuro	Aizu Sinkuro	"
25	Sinkuro	Wase Marunasu	"
26	Wase Hetamurasaki	Sinkuro	"
27	Tiba Wase	Sinkuro	"
28	Sironasu	Kawabe Naganasu	"
29	Sironasu	Urawa Sinkuro 2–g_o	1925
30	Siro 13–g_o	Sinkuro	"
31	Kintyaku	Urawa Sinkuro 2–g_o	"
32	Sinkuro	Turuboso Sennari	"
33	Sinkuro	Barazima A	"
34	Sinkuro	Minden	"
35	Sinkuro	Kubota	"
36	Sinkuro	Suzunari	"
37	Sinkuro	Yahara	"
38	Sinkuro	Yokono Sennari	"
39	Sinkuro	Furukawa	"
40	Sinkuro	Tiba Wase C	"
41	Sironasu	Tiba Wase C	"

one, No. 20, showing −0.23 gram and +59 percent. With all crosses, the coefficient of correlation is $+0.519 \pm 0.093$.

Discussion

Concerning the immediate effect of cross-pollination on the size of seed, many instances have been reported with maize. COLLINS (1909) reported that 21 F_1 seeds on a plant of the small-seeded Chinese maize had an average weight of 0.178 gram, while the selfed seeds from the same part of the same ear had that of 0.153 gram. COLLINS and KEMPTON (1913) pollinated various maize varieties having white seeds with a mixture of

TABLE 2

The weight of 1,000 grains of the F_1 seed and the selfed seed of the parents.

CROSS NO.	F_1 SEED gm	SELFED SEED		DIFFERENCE OF POLLEN PARENT FROM MOTHER PARENT gm	PERCENT INCREASE OF F_1 OVER MOTHER PARENT
		MOTHER PARENT gm	POLLEN PARENT gm		
4	4.69	3.09	4.98	+1.89	+52
5	4.29	3.12	4.98	+1.86	+38
6	4.90	2.98	4.98	+2.00	+71
7	4.17	3.76	4.98	+1.22	+11
8	4.50	3.57	4.98	+1.41	+26
9	5.40	4.45	4.98	+0.53	+21
11	4.91	4.04	5.75	+1.71	+22
12	4.32	3.41	5.75	+2.34	+27
13	5.30	4.70	5.75	+1.05	+13
15	4.16	3.12	4.04	+0.92	+33
17	4.53	3.71	4.70	+0.99	+22
19	3.26	2.98	4.29	+1.29	+ 9
20	4.75	2.98	2.75	−0.23	+59
21	3.86	2.98	3.95	+0.97	+30
22	4.00	4.29	2.75	−1.54	− 7
24	3.73	3.53	3.95	+0.42	+ 6
25	3.22	3.53	4.40	+0.87	− 9
27	2.75	2.75	3.53	+0.78	0
28	3.56	2.98	4.23	+1.25	+19
32	3.73	3.96	4.87	+0.91	− 6
34	3.69	3.96	3.55	−0.41	− 7
35	4.55	3.96	4.82	+0.86	+15
36	4.47	3.96	4.53	−0.57	+13
37	4.05	3.96	4.01	+0.05	+ 2
38	4.29	3.96	3.72	−0.24	+ 8
39	4.26	3.96	4.00	+0.04	+ 8
40	3.88	3.96	4.16	+0.20	− 2
41	4.36	3.15	4.16	+1.01	+38
Average					+18.2

their own pollen and pollen from a colored-seeded variety, and obtained a total of 1,658 hybrid seeds to be compared with 3,513 selfed seeds from eleven ears involving five varieties. The increase in weight of the F_1 seeds was 8.8 percent in average ranging from 2.8 to 21.1 percent. CARRIER (1913) reported the average weight of 6,000 maize seeds each of F_1 and selfed to be 2.104 and 1.792 grams, respectively, showing an increase of 17.4 percent, and that, in a cross between different pure-bred strains of the same variety, he obtained even a 30 percent increase. He (1919) also pointed out the fact that mixtures of seeds of different strains of maize give higher yields than seeds of a single strain, and explained this fact as due to the immediate increase in weight of crossed seeds. WOLFE (1915), by using mixed pollen in 31 maize crosses, obtained mixtures of F_1 and selfed seeds. As compared in average weight with the selfed seeds, the F_1 seeds increased in 23 crosses but decreased in the other 8 crosses

TABLE 3

Variation in the increase or decrease in weight of the F_1 seed.

PERCENT INCREASE OR DECREASE	−5 to 0	0 to 5	5 to 10	10 to 15	15 to 20	20 to 25	25 to 30	30 to 35	35 to 40	40 to 45	45 to 50	50 to 55	55 to 60	60 to 65	65 to 70
Number of crosses	4	2	1	4	4	1	3	3	1	2	.	.	1	1	.	.	1

and exceeded in total average by 2.8 percent. JONES (1918) obtained an average increase of 19.2 percent in two crosses of maize.

GRIFFEE (1922), with wheat, pollinated a part of emasculated spikes with pollen from other plants of the same pure line, and the rest on the same plant with pollen from another variety or species. Among seven crosses thus made, three increased in average weight from 3.0 to 7.6 percent over the uncrossed seeds, while none of the other four showed any appreciable difference from the uncrossed ones.

With beans, TSCHERMAK (1922) reported two cases of the immediate effect on the size of seed due to cross-pollination: one in which average weights were 0.10026 gram in the selfed seed of the mother parent and 0.7415 gram in that of the pollen parent, while 0.342 gram in the F_1 seed; and the other in which there were 0.10026 gram in the selfed seed of the mother parent and 0.5732 gram in that of the pollen parent, while there were 0.1961 gram in the F_1 seed. SIRKS (1925), who made an extensive study of bean crosses, has an opinion that in certain cases the crossed seed may decrease in weight under the selfed seed of the mother parent. He said that "if the pollen parent is of a light and white-seeded race, while the mother parent is a colored and heavy-seeded one, then the

F_1 seeds will be more or less intermediate." WINGARD (1927), making reciprocal crosses of six combinations of bean varieties, found a marked increase in weight of the F_1 seed in one of these crosses, while in its reciprocal cross and the crosses of the other five combinations, no apparent difference was seen from the selfed seeds of the mother parents. In the particular cross just mentioned, the selfed seed of the mother parent had an average weight of 0.694 gram and that of the pollen parent 0.420 gram, while the F_1 seed had an average of 1.076 grams. In this case the increase was 55.0 percent, notwithstanding that the seed of the pollen parent was smaller than that of the mother parent.

In the egg-plants used in the present experiment, the F_1 seed of most crossings gave an immediate increase in weight over the selfed seed of the mother parent. Contrasting to SIRKS's results with beans we can not find any combination in which the weight of the F_1 seed was significantly below that of the selfed seed of the mother parent. Although there are a few crosses in which the F_1 seed somewhat decreased in weight, it is not evident that the decrease was due to the small weight of the seed of the pollen parent. WINGARD obtained similar results with beans, contrary to SIRKS's opinion, already cited.

The result of the present study shows a positive correlation ($r = +0.519 \pm 0.093$) between the difference in weight of the seed of the pollen parent from that of the mother parent and the increase in weight of the F_1 seed, but there is a marked exception in No. 20. It must be concluded that the increase in weight of the F_1 seed has a tendency to be influenced positively by the weight of seed of the pollen parent, but the tendency is not great.

It is quite apparent that the increase in weight of the F_1 seed of the egg-plant is due to the increased size of the embryo and is a manifestation of hybrid vigor. The variation in the amount of increased weights is regarded as being due to differences in heterozygosity of the growth factors of the embryo, as well as to differences in the pericarp, which is not strictly a part of the seed but is of purely maternal origin.

THE DIAMETER OF STEM AND THE HEIGHT OF PLANT

The diameter of stem

Twenty mature plants each, of the hybrid and parental strains, were measured at the flat diameter of the internode between the node of the cotyledons and that of the primary leaf. The average result is shown in table 4, in which 28 combinations of crosses instead of 41 are given, as this measurement was not made in the 1925 culture.

TABLE 4

The diameter of stem.

CROSS NO.	F_1 mm	MOTHER PARENT mm	POLLEN PARENT mm	AVERAGE OF PARENTS mm	PERCENT INCREASE OR DECREASE OF F_1 AS COMPARED WITH		
					THINNER PARENT	AVERAGE OF PARENTS	THICKER PARENT
1	16.1	18.3	15.6	16.9	+ 3	− 5	−12
2	13.2	13.3	15.6	14.4	− 1	− 8	−15
3	15.4	13.3	13.3	13.3	+15	+15	+15
4	13.8	12.9	12.3	12.6	+12	+10	+ 7
5	13.4	11.0	12.3	11.6	+22	+16	+ 9
6	14.0	11.7	12.3	12.0	+20	+17	+14
7	12.6	10.2	12.3	11.2	+24	+12	+ 2
8	12.1	10.8	12.3	11.5	+12	+ 5	− 2
9	13.1	11.7	12.3	12.0	+12	+ 9	+ 7
10	9.3	9.0	12.3	10.6	+ 3	− 2	−24
11	12.7	10.3	13.1	11.7	+23	+ 9	+ 3
12	13.6	9.0	13.1	11.0	+51	+24	+ 4
13	14.4	12.3	13.1	12.7	+17	+13	+10
14	12.4	13.1	11.9	12.5	+ 4	− 1	− 5
15	13.4	11.0	10.3	10.6	+30	+26	+22
16	10.8	10.2	12.9	11.5	+ 6	− 6	−16
17	13.4	10.9	12.3	11.6	+23	+16	+ 9
18	13.5	11.9	12.3	12.1	+13	+12	+10
19	16.6	17.9	14.6	16.2	+14	+ 3	− 7
20	16.0	17.9	16.1	17.0	− 1	− 6	−11
21	16.6	17.9	16.0	16.9	+ 4	− 2	− 7
22	15.9	14.6	16.1	15.3	+ 9	+ 4	− 1
23	15.3	14.6	16.0	15.3	+ 5	0	− 4
24	15.8	15.2	16.0	15.6	+ 4	+ 1	− 1
25	15.9	15.2	15.2	15.2	+ 5	+ 5	+ 5
26	16.3	16.3	15.2	15.7	+ 7	+ 3	0
27	15.2	16.1	15.2	15.6	0	− 3	− 6
28	16.4	17.9	13.3	15.6	+23	+ 5	− 8
Average					+14.4	+ 5.8	−0.3

As compared with the parent having the thinner stem, crosses range from −1 to +51 percent, averaging +14.4 percent. There are 2 crosses thinner, 1 cross same and 25 crosses thicker. As compared with the median diameter of both parents crosses range from −12 to +26 percent averaging +5.8 percent, and there are 8 crosses thinner, 1 cross same and 19 crosses thicker. Finally, as compared with the thicker parent, crosses range from −24 to +22 percent averaging −0.3 percent, and there are 15 crosses thinner, 1 cross same and 12 crosses thicker. These variations are given in table 5.

TABLE 5

Variation in the increase or decrease of F_1 in the diameter of stem.

PERCENT INCREASE OR DECREASE	−20	−15	−10	−5	0	5	10	15	20	25	30	35	40	45	50
As compared with thinner parent				3	7	3	6	2	5	1	.	.	.	.	1
As compared with average of parents			1	4	4	7	3	4	3	1	1				
As compared with thicker parent	1	2	2	5	6	3	6	2	.	1					

The amount of decrease in the two crosses which are thinner than the thinner parent is only 1 percent in both cases, and it may be regarded that these crosses and the respective thinner parents are generally of the same diameter.

The fact that, in total average, the cross is only 0.3 percent thinner than and very near to the thicker parent, appears to show that the thicker stem may be almost complete dominant genetically over the thinner one. To make an analytical study of the variation in increased or decreased rates of crosses as compared with the thicker parents, a comparison between the variation and the distribution of the normal curve[2] is given in table 6.

The table shows that the observed variation agrees well with the distribution of the normal curve. This agreement, however, does not prove that the variation is attributed merely to a chance fluctuation, but shows that there remains a question whether it is attributed to a simple fluctuation or is concerned with some internal causes. We have not here any evidence to decide this question. If the variation is attributed to a simple fluctuation, it is very difficult to assume two or more allelomorphic pairs governing the thickness of the stem. And yet, in fact, the existence of various varieties showing various thickness of stems proves that the allelomorphs under consideration are not simple. Hence, it may be said that the variation in increased or decreased rates in the stem-diameter of crosses is concerned with the amount of heterozygosity.

The height of plant

The same plants as were measured for stem-diameter were also measured for height. Table 7 gives the average result.

As compared with the shorter parent, the crosses range from −6 to

[2] The distribution of the normal curve was calculated by the formula: $y_x = \frac{n}{\sigma\sqrt{2\pi}} \cdot \frac{1}{e^{x^2/2\sigma^2}}$,

where y = the frequency of the normal curve, x = the difference of any class value from the median σ = the standard deviation, and n = the total number of the crosses studied.

+40 percent, averaging +12.9 percent, and there are 3 crosses shorter, 1 cross same and 24 crosses taller. As compared with the median height of both parents, the crosses range from −11 to +26 percent, averaging +6.4 percent, and there are 6 crosses shorter, 1 cross same and 21 crosses taller. Moreover, as compared with the taller parent, the crosses range from −24 to +18 percent, averaging +1.1 percent, and there are 13 crosses shorter, 2 crosses same and 13 crosses taller. All these variations are shown in table 8.

TABLE 6

Comparison between the variation in the difference of F_1 from the thicker parent in the diameter of stem and the distribution of the normal curve.

PERCENT INCREASE OR DECREASE	NO. CROSSES	DISTRIBUTION OF THE NORMAL CURVE	DEVIATION	PROBABLE ERROR	DEV./P.E.
−20	1	1.1	−0.1	±0.69	0.1
−15	2	2.3	−0.3	±0.98	0.3
−10	2	3.9	−1.9	±1.23	1.5
− 5	5	5.2	−0.2	±1.39	0.1
0	6	5.4	+0.6	±1.41	0.4
5	3	4.5	+1.5	±1.31	1.1
10	6	2.9	+3.1	±1.09	2.8
15	2	1.5	+0.5	±0.80	0.6
20	.	0.6	−0.6	±0.52	1.2
	1	0.2	+0.8	±0.30	2.7

NAGAI and KIDA (1926), from their study of seven F_1 crosses of egg-plants, found that the increase in height varied considerably; some crosses averaged 11 percent increase over the median height of both parents, while with others the average height was just the same as the taller parent. The author's result is similar in these points.

The fact that the average height of F_1 crosses is actually the same as that of the taller parent appears to show also, just as in the case of the stem-diameter, that the tallness may be almost perfectly dominant genetically over the shortness. Hence, by the same manner as in the case of the stem-diameter, a comparison is made in table 9 between the variation of crosses and the distribution of the normal curve.

TABLE 7

The height of plant.

CROSS NO.	F_1 mm	MOTHER PARENT mm	POLLEN PARENT mm	AVERAGE OF PARENTS mm	PERCENT INCREASE OR DECREASE OF F_1 AS COMPARED WITH		
					SHORTER PARENT	AVERAGE OF PARENTS	TALLER PARENT
1	103.8	92.7	100.2	96.4	+12	+ 8	+ 4
2	90.0	95.7	100.2	97.9	− 6	− 8	−10
3	108.0	95.7	76.2	85.9	+40	+26	+13
4	94.3	74.2	79.8	77.0	+27	+22	+18
5	93.4	78.9	79.8	79.3	+18	+18	+17
6	91.3	86.3	79.8	83.0	+14	+10	+ 6
7	79.5	67.8	79.8	73.8	+17	+ 8	0
8	85.8	79.1	79.8	79.4	+ 8	+ 8	+ 8
9	89.6	73.5	79.8	76.6	+22	+17	+12
10	61.0	57.9	79.8	68.0	+ 4	−11	−24
11	72.3	65.3	75.7	70.5	+11	+ 3	− 4
12	81.3	57.9	75.7	66.8	+40	+22	+ 7
13	83.5	75.3	75.7	75.5	+11	+11	+10
14	75.5	75.7	66.1	70.9	+14	+ 6	0
15	73.9	78.9	65.3	72.1	+13	+ 2	− 6
16	68.2	67.8	74.2	71.0	+ 1	− 4	− 8
17	78.2	64.1	75.3	69.7	+22	+12	+ 4
18	79.3	66.1	79.8	72.9	+20	+ 8	− 1
19	89.9	88.0	79.3	83.1	+13	+ 8	+ 2
20	86.8	88.0	83.2	85.6	+ 4	+ 1	− 1
21	78.6	88.0	70.0	79.0	+12	− 1	−11
22	87.2	79.3	83.2	81.2	+10	+ 7	+ 5
23	80.5	79.3	70.0	74.6	+15	+ 8	+ 2
24	82.9	84.1	70.0	77.0	+18	+ 8	− 1
25	68.7	84.1	70.7	77.4	− 3	−11	−18
26	83.5	83.1	84.1	83.6	0	0	− 1
27	82.6	83.2	84.1	83.6	− 1	− 1	−12
28	92.8	88.0	93.7	90.8	+ 5	+ 2	− 1
Average					+12.9	+ 6.4	+0.4

TABLE 8

Variation in the increase or decrease of F_1 in the height of plant.

PERCENT INCREASE OR DECREASE	−20	−15	−10	−5	0	5	10	15	20	25	30	35
As compared with shorter parent				1	3	4	2	9	4	2	1	. 2
As compared with average of parents			2	1	4	4	10	2	2	2	1	
As compared with taller parent	1	1	2	2	9	5	4	2	2			

Here also the agreement is good; and as to the question whether the variation is attributed simply to a chance fluctuation or is due to some other causes, we have to apply the same reasoning to this case also. Thus,

TABLE 9

Comparison between the variation in the difference of F_1 from the taller parent in height of plant and the distribution of the normal curve.

PERCENT INCREASE OR DECREASE	NO. CROSSES	DISTRIBUTION OF THE NORMAL CURVE	DEVIATION	PROBABLE ERROR	DEV./P.E.
−20	1	0.8	−0.2	±0.59	0.3
−15	1	1.9	−0.9	±0.90	1.0
−10	2	3.6	−1.6	±1.19	1.3
−5	2	5.2	−3.2	±1.39	2.3
0	9	5.8	+3.2	±1.45	2.2
5	5	4.9	+0.1	±1.36	0.1
10	4	3.2	+0.8	±1.13	0.7
15	2	1.6	+0.4	±0.83	0.5
	2	0.6	+1.4	±0.52	2.7

as the existence of various varieties of egg-plants having various heights proves that the allelomorphs of the height are not simple, the variation in the increased or decreased rates in height of crosses is regarded as being associated with differences in heterozygosity.

TABLE 10

Comparison between the increase or decrease in the diameter of stem and that in the height of plant in F_1.

AS COMPARED WITH	CHARACTER	PERCENT INCREASE OR DECREASE			NUMBER OF CROSSES		
		MINIMUM	MAXIMUM	AVERAGE	POORER	SAME	BETTER
Parent of poorer value	Diameter of stem	− 1	+51	+14.4	2	1	25
	Height of plant	− 6	+40	+12.9	3	1	24
Average of parents	Diameter of stem	−12	+26	+ 5.8	8	1	19
	Height of plant	−11	+26	+ 6.4	6	1	21
Parent of better value	Diameter of stem	−24	+22	− 0.3	15	1	12
	Height of plant	−24	+18	+ 0.4	13	2	13

TABLE 11

Number of days from the sowing till the first harvesting.

CROSS NO.	F_1	MOTHER PARENT	POLLEN PARENT	DIFFERENCE BETWEEN PARENTS	AVERAGE OF PARENTS	F_1 AS COMPARED WITH		
						LATE PARENT	AVERAGE OF PARENTS	EARLY PARENT
1	127	130	123	7	126.5	− 3	+ 0.5	+ 4
2	130	144	123	21	133.5	−14	− 3.5	+ 7
3	130	144	123	21	133.5	−14	− 3.5	+ 7
4	120	143	120	23	131.5	−23	−11.5	0
5	126	138	120	18	129.0	−12	− 3.0	+ 6
6	130	143	120	23	131.5	−13	− 1.5	+10
7	119	119	120	1	119.5	− 1	− 0.5	0
8	124	141	120	21	130.5	−17	− 6.5	+ 4
9	136	147	120	27	133.5	−11	+ 2.5	+16
10	137	137	120	17	128.5	0	+ 8.5	+17
11	119	119	119	0	119.0	0	0	0
12	119	137	119	18	128.0	−18	− 9.0	0
13	119	134	119	15	126.5	−15	− 7.5	0
14	119	119	119	0	119.0	0	0	0
15	119	138	119	19	128.5	−19	− 9.5	0
16	133	119	143	24	131.0	−10	+ 2.0	+14
17	130	145	134	11	139.5	−15	− 9.5	− 4
18	119	119	120	1	119.5	− 1	− 0.5	0
19	125	126	126	0	126.0	− 1	− 1.0	− 1
20	115	126	120	6	123.0	−11	− 8.0	− 5
21	120	926	119	7	122.5	− 6	− 2.5	+ 1
22	120	126	120	6	123.0	− 6	− 3.0	0
23	115	126	119	7	122.5	−11	− 7.5	− 4
24	115	120	119	1	119.5	− 5	− 4.5	− 4
25	122	120	120	0	120.0	+ 2	+ 2.0	+ 2
26	122	123	120	3	121.5	− 1	+ 0.5	+ 2
27	115	120	120	0	120.0	− 5	− 5.0	− 5
28	123	126	125	1	125.5	− 3	− 2.5	− 2
29	121	132	121	11	126.5	−11	− 5.5	0
30	121	131	123	8	127.0	−10	− 6.0	− 2
31	120	127	121	6	124.0	− 7	− 4.0	− 1
32	115	123	115	8	119.0	− 8	− 4.0	0
33	123	123	117	6	120.0	0	+ 3.0	+ 6
34	120	123	117	6	120.0	− 3	0	+ 3
35	117	123	118	5	120.5	− 6	− 3.5	− 1
36	120	123	117	6	120.0	− 3	0	+ 3
37	120	123	124	1	123.5	− 4	− 3.5	− 3
38	120	123	120	3	121.5	− 3	− 1.5	0
39	120	123	126	3	124.5	− 6	− 4.5	− 3
40	117	123	120	3	121.5	− 6	− 4.5	− 3
41	117	132	120	12	126.0	−15	− 9.0	− 3
Average				9.2		− 7.7	− 3.1	+ 1.5

Relation between the diameter of stem and the height of plant

It may be remembered that there is a close analogy between the amount of increase or decrease in the diameter of stem and that of the height of plant of the cross. Table 10 shows this relation. To see whether or not the analogy is due to an association in the development of both the characters, a coefficient of correlation has been calculated: $r = +0.581 \pm 0.085$. It is seen that there is an appreciable positive correlation, though not so close as might be expected from table 10.

TIME OF FIRST HARVESTING

Table 11 gives average days from sowing till the first harvesting of each of forty-one crosses and their parental strains. When compared with the late parent, crosses range from -23 to $+2$ days averaging -7.7 days, and there are 36 crosses earlier, 4 crosses same and only 1 cross later. As compared with the median time of both parents, crosses range from -11.5 to $+8.5$ days averaging -3.1 days, and there are 30 crosses earlier, 4 crosses same and 7 crosses later. Further, when compared with the early parent, crosses range from -5 to $+17$ days averaging $+1.5$ days, and there are 14 crosses earlier, 12 crosses same and 15 crosses later. Table 12 shows these variations.

From the first result we observe that the average difference of the first-harvesting time between both parents of all the crossings studied is 9.2 days (table 11), and that the crosses average 7.7 days earlier than the late parent and 1.5 days later than the early parent. The crosses on the average incline 83.7 percent from the late parent towards the early parent and 16.3 percent from the early parent towards the late one.

It is a well-known fact with various plants that the growth or maturity is often hastened as a phenomenon of heterosis. NAGAI and KIDA (1926) reported, from their study of ten crosses of egg-plants, that the first-

TABLE 12

Variation in the first-harvesting time of F_1.

NUMBER OF DAYS	−23—25	−20—22	−17—19	−14—16	−11—13	−8—10	−5—7	−2—4	−1—+1	2—4	5—7	8—10	11—13	14—16	17—19
As compared with late parent	1	.	3	5	6	3	8	6	8	1					
As compared with average of parents					1	7	7	12	9	4	.	1			
As compared with early parent							2	9	16	6	4	1	.	2	1

harvesting time was earlier than the average of both parents in all crosses except only one, averaging 6.9 days earlier; and that even as compared with the early parent, six crosses were earlier and the average of all the ten crosses was 3.16 days earlier. The author's result agrees well with this. The time of first harvest in the crosses was hastened as compared to the parents in most cases and the degree of hastening varied widely in different crosses. The hastening, in the plants grown by the writer, however, was about four days less on the average than in the results obtained by NAGAI and KIDA either when compared with the average of both parents or when compared with the early parent.

With tomatoes which belong to the same family as egg-plants, HAYES and JONES (1916) found that a cross between Stone and Dwarf Champion matured somewhat earlier than the early parent.

It may be concluded that (1) the degree of hastening in fruit production of egg-plant crosses is widely different according to different combinations of varieties, (2) the cross is earlier than the average of both parents in a majority of the cases, and that (3) often the cross is earlier even than the early parent.

YIELD

General result

Fruits of all the plants of crosses as well as of the parental strains were harvested at two or three day intervals throughout the yielding period. The average yield per plant is given in table 13.

When compared with the poorer parent, crosses yielded from 1.3 to 222.2 percent more, averaging 69.9 percent more, and all crosses exceeded in yield without exception. When compared with the average yield of both parents, crosses range from −43.7 to +152.0 percent averaging +36.1 percent, and only four crosses yielded less while the other 37 crosses yielded more. Further, as compared with the better parent, crosses range from −61.1 to +140.8 percent averaging +17 percent, and there are 12 less-yielding crosses contrasting to 29 more-yielding ones. These variations are shown in table 14.

Relation between the yield of parents and that of crosses

Correlations are here studied between the yield of the poorer parent and that of the cross, between the average yield of both parents and the yield of the cross, and between the yield of the better parent and that of the cross. Coefficients of the correlations have been calculated:

TABLE 13
Yield per plant.

CROSS NO.	F_1 gm	MOTHER PARENT gm	POLLEN PARENT gm	AVERAGE OF PARENTS gm	PERCENT INCREASE OR DECREASE OF F_1 AS COMPARED WITH		
					POORER PARENT	AVERAGE OF PARENTS	BETTER PARENT
1	1,804	1,755	1,440	1,597	+25.3	+ 13.0	+ 2.8
2	1,069	1,035	1,440	1,237	+ 3.3	− 14.6	− 25.8
3	1,714	1,035	532	783	+222.2	+118.9	+ 65.6
4	2,053	1,077	1,023	1,050	+100.7	+ 95.5	+ 90.6
5	1,345	642	1,023	832	+109.5	+ 61.7	+ 31.5
6	1,478	684	1,023	853	+116.1	+ 73.3	+ 44.5
7	1,124	658	1,023	840	+ 70.8	+ 33.8	+ 9.9
8	1,293	688	1,023	855	+ 87.9	+ 51.2	+ 26.4
9	1,198	426	1,023	734	+181.2	+ 63.2	+ 17.1
10	398	393	1,023	708	+ 1.3	− 43.7	− 61.1
11	729	392	1,012	702	+ 86.0	+ 3.8	− 28.0
12	830	393	1,012	702	+111.2	+ 18.2	− 18.0
13	1,022	536	1,012	774	+ 90.7	+ 32.0	+ 1.0
14	749	1,012	431	721	+ 73.8	+ 3.9	− 26.0
15	895	642	392	517	+128.3	+ 73.1	+ 39.4
16	933	658	1,077	867	+ 41.8	+ 7.6	− 13.4
17	1,416	588	536	562	+164.2	+152.0	+140.8
18	1,073	431	1,023	727	+149.0	+ 47.6	+ 5.0
19	2,136	1,685	1,235	1,460	+ 23.0	+ 46.3	+ 26.8
20	2,129	1,685	1,362	1,523	+ 56.3	+ 39.8	+ 26.4
21	2,034	1,685	1,228	1,456	+ 65.6	+ 39.7	+ 20.7
22	1,754	1,235	1,362	1,298	+ 42.0	+ 35.1	+ 28.8
23	1,748	1,235	1,228	1,231	+ 42.3	+ 42.0	+ 41.5
24	1,825	1,534	1,228	1,381	+ 48.6	+ 32.1	+ 19.0
25	1,499	1,534	1,492	1,513	+ 0.5	− 0.9	− 2.3
26	2,103	1,843	1,534	1,688	+ 37.0	+ 24.6	+ 14.1
27	1,440	1,362	1,534	1,448	+ 5.7	− 0.6	− 6.1
28	2,139	1,685	912	1,298	+139.1	+ 64.8	+ 26.9
29	1,976	2,319	1,532	1,926	+ 29.0	+ 2.6	− 14.8
30	2,714	1,668	1,777	1,722	+ 62.7	+ 57.6	+ 52.7
31	2,011	2,059	1,532	1,795	+ 31.3	+ 12.0	− 2.3
32	1,983	1,777	739	1,258	+ 68.3	+ 57.6	+ 11.6
33	1,610	1,777	1,421	1,599	+ 13.3	+ 0.7	− 9.4
34	2,419	1,777	1,242	1,509	+ 94.8	+ 60.6	+ 36.1
35	2,605	1,777	1,759	1,768	+ 48.1	+ 47.3	+ 46.6
36	2,077	1,777	1,474	1,625	+ 40.9	+ 27.8	+ 16.9
37	2,141	1,777	2,091	1,934	+ 20.5	+ 10.7	+ 2.4
38	1,676	1,777	1,341	1,559	+ 24.9	+ 7.5	− 5.7
39	2,369	1,777	1,834	1,805	+ 33.3	+ 31.2	+ 29.2
40	2,073	1,777	1,750	1,763	+ 18.5	+ 17.6	+ 16.7
41	2,742	2,319	1,750	2,034	+ 56.7	+ 34.8	+ 18.2
Average					+ 69.9	+ 36.1	+ 17.0

Poorer parent and cross	$= +0.800 \pm 0.038$
Average of both parents and cross	$= +0.813 \pm 0.036$
Better parent and cross	$= +0.719 \pm 0.051$

We see here that the yield of the cross has a close positive relation with that of either parent, and especially with the average yield of both parents.

Relation between the yield of parents and the increased yield of crosses

A correlation coefficient between the average yield of both parents and the rate of increased yield of the cross over the former was -0.354 ± 0.083. This result shows that the increase in yield of the cross bears a negative relation with the yield of parents, but the relation can not be considered at all marked as the coefficient is only 4.3 times the size of probable error.

TABLE 14

Variation in the yield per plant of F_1.

PERCENT INCREASE OR DECREASE	−60	−40	−20	0	20	40	60	80	100	120	140	160	180	200	220
As compared with poorer parent				6	8	8	4	4	4	2	1	2	1	.	1
As compared with average of parents		1	.	3	11	10	7	6	1	1	.	1			
As compared with better parent	1	.	3	8	12	10	4	1	1	.	.	1			

Another correlation is studied between the difference in yield of both parents and the rate of increased yield of the cross over the average yield of both parents. The coefficient is -0.128 ± 0.099. There is no evidence here of correlation.

Relation of other characters on the increase in yield of crosses

From table 13, we find 17 crosses which exceeded the better parents in yield by 20 percent or more. Table 15 shows these crosses being accompanied in part by certain apparent characteristics of parents.

From the table, the following relations between characteristics of both parents are seen:

Group I (with 2 crosses) . . . . there is a wide difference in the color of fruit and vegetative part.

Group II (with 1 cross) . . . . there are wide differences in the color of fruit and vegetative part and the shape of fruit.

Group III (with 9 crosses) . . . . there are wide differences in the shape of fruit and the amount of pubescence of vegetative part.

Group IV (with 3 crosses) . . . . there are wide differences in the color of fruit and vegetative part, the shape of fruit, and the amount of pubescence of vegetative part.

Group V (with 2 crosses) . . . . there is no wide difference.

It is interesting to see that, thus, most of the crosses which exhibited material increases in yield were from parents which differed widely from each other, although there were a few crosses not showing such a remarkable increase in yield in spite of the parents being of diverse types.

Discussion

Ten crosses of egg-plants made by NAGAI and KIDA (1926) exceeded the average yield of both parents by from 1 to 71 percent averaging 33 percent. Even as compared with the better parent, most of them yielded more and the average increase of all the crosses was 15 percent. Of two crosses reported by TATEISI (1927) one exceeded the better parent in yield by 8 percent, while the other did not excel.

WELLINGTON (1912) reported that a tomato cross yielded 24.3 pounds per plant, while the mother and pollen parents yielded 13.1 and 21.1 pounds, respectively. Of two tomato crosses made by HAYES and JONES (1916), one averaged 15 percent more yield than the better parent, while the other gave no apparent increase of yield.

Among many reports as to the hybrid vigor in maize crosses some most important ones are cited here, and the case of egg-plants is studied comparatively. JONES and his coworkers (1917), comparing fifty crosses with their parents, said that "the highest yielding parents gave the highest yielding crosses as would be expected, but a rather unexpected result was obtained in that there was apparently no relation between the yield of the parents and the increase in the yield of the cross." RICHEY (1925), who compared seventy crosses between inbred lines of maize with their parents, reported that there was no relation between the productiveness of the inbred lines and the yield of their crosses. The present case of egg-plant crosses, corroborating actually the conclusion of JONES and his coworkers though the kind of plants differs, shows that the positive correlation is very close between the yield of the parents and that of the cross, but there is no apparent relation, or is rather a slight negative correlation, between the yield of the parents and the increase in yield of the cross.

JONES and his coworkers stated also that, with maize, "there was a tendency for the crosses whose parents differed in their ability to yield to give the greatest increase." On this point, the present result of egg-plants gives an adverse conclusion that there is apparently no relation between

TABLE 15

Combinations whose F_1 crosses exceeded in yield the better parents by 20 percent or more.

GROUP	CROSS NO.	MOTHER PARENT				POLLEN PARENT			
		NAME OF VARIETY	COLOR OF FRUIT AND VEGETATIVE PART	SHAPE OF FRUIT	PUBESCENCE ON VEGETATIVE PART	NAME OF VARIETY	COLOR OF FRUIT AND VEGETATIVE PART	SHAPE OF FRUIT	PUBESCENCE OF VEGETATIVE PART
I	30	Siro 13-*gô*	Green	Oval	Less	Sinkuro	Black	Oval	Less
	19	Sironasu	"	Round and ribbed	Much	Kintyaku	"	Round and ribbed	Much
II	28	Sironasu	Green	Round and ribbed	Much	Kawabe Naganasu	Black	Long	Much
III	3	Kawabe Naganasu	Black	Long	Much	Turuboso Sennari	Black	Oval	Less
	6	" "	"	"	"	Sinkuro	"	"	"
	5	Kintyaku	"	Round and ribbed	"	"	"	"	"
	15	"	"	"	"	Turuboso Sennari	"	"	"
	22	"	"	"	"	Tiba Wase	"	"	"
	23	"	"	"	"	Aizu Sinkuro	"	"	"
	8	Yuiki Yamanasu	"	"	"	Sinkuro	"	"	"
	34	Sinkuro	"	Oval	Less	Minden	"	Round and ribbed	Much
	35	"	"	"	"	Kubota	"	"	"
IV	4	Sironasu	Green	Round and ribbed	Much	Sinkuro	Black	Oval	Less
	20	"	"	"	"	Tiba Wase	"	"	"
	21	"	"	"	"	Aizu Sinkuro	"	"	"
V	17	Wase Hetamurasaki	Black	Oval	Less	Wase Sennari	Black	Oval	Less
	39	Sinkuro	"	"	"	Furukawa	"	"	"

the difference in yield of both parents and the increase in yield of the cross, the correlation coefficient being -0.128 ± 0.099 as already stated.

It is a well-known fact that the cross between varieties of diverse types tends to give a greater degree of hybrid vigor. In the case of egg-plants also, most of the crosses which exhibited significant increases in yield were given by combinations of the varieties differing widely in type from each other. This fact is in agreement with the assumption advocated by EAST and JONES (1919) that hybrid vigor is the result of the bringing together of the greatest number of favorable growth factors.

RELATION BETWEEN THE FIRST-HARVESTING TIME AND THE YIELD

It has been already stated that most of the crosses of the present study apparently had tendencies to hasten the time of production and to increase the yield. To see whether or not the hastening of the first-harvesting time and the rate of increased yield of crosses associate mutually, a correlation between them is studied. The coefficient was -0.417 ± 0.087; we see here a somewhat appreciable negative correlation. In other words, there is a tendency for the crosses which give greater increases in yield to show greater degrees of hastening in the time of production. This fact is important and convenient for practical utilization of the first generation hybrid of egg-plants.

F_1 EXPRESSIONS OF OTHER CHARACTERS

Some other visible characters were observed besides those mentioned above. The result is briefly summarized as follows:

1. The branching habit.—In some varieties the branches expand almost horizontally, while in some other varieties they grow erectly. There are various types of branching habits almost continuously between these two types. The F_1 cross exhibited a more or less intermediate type between both parents but rather inclined towards the more erect one.

2. The size of leaflet.—The cross was about intermediate of both parents.

3. The shape of fruit.—According to different varieties, there are various shapes of fruits from almost round or somewhat flat types to very long ones. In every case, the cross showed an intermediate type. In some varieties the fruits are ribbed. In crossing between such a variety and a one bearing smooth fruits, the F_1 fruit was smooth when the ribs of the one parent were slight, but somewhat ribbed when they were conspicuous.

4. The color of fruit.—There are two main types, black and white. The former shows black or dark purple coloration on the skin of unripe

fruits as well as on the vegetative part, while the latter exhibits no such coloration. The writer (1924) has shown that these characters depend on a single factor difference, the black being dominant over the white.

5. The spine on the calyx.—Egg-plant varieties have various numbers of spines on the calyx. The cross between two varieties differing in this respect inclined towards a less-spined type.

FIGURE 1.—Seedlings of a cross of egg-plants having practical value. Above, Kintyaku; below, Sinkuro; the F_1 cross between them. This cross is very vigorous and productive.

CROSSES BEING USED FOR PRACTICAL PURPOSES

For the practical use of the F_1 cross of egg-plants, it should be superior in the suitability of shape and quality of fruit for marketing and some other points besides the yielding ability and the time of production. It

is desirable also that the crossed seed may be easily produced. In the oval type one fruit gives about 800 seeds and in the long type far less, while 2,000 or more seeds are obtained per fruit in the round type.

From these points of view, two crosses, Sironasu×Sinkuro and Kintyaku×Sinkuro, among the crosses studied were determined as the most superior ones for the commercial use. These two crosses are very vigorous and robust from the start (see figure 1) and correspondingly their seedlings are grown quite easily. The fruits are glossy black in color, oval in shape (see figure 2), and thick in flesh structure, all these characters being suitable for markets in Tokyo—most products of vegetable crops in the

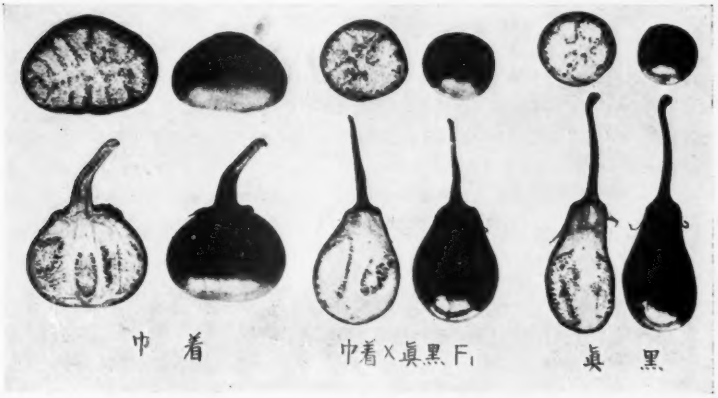

FIGURE 2.—Fruits of a cross of egg-plants having practical value. At left, Kintyaku; at right, Sinkuro; the F_1 cross between them.

prefecture Saitama are supplied to Tokyo. Moreover, it facilitates the practical use of these crosses that both parental varieties produce about 2,500 seeds per fruit on the average.

In regard to yielding abilities of these crosses, a trial was made for four years in comparison with Sinkuro which is the most universal variety in the prefecture. As shown in table 16, the two crosses increased by 75.7 and 50.8 percent, respectively, over Sinkuro in average yield of the 4-years test. The crosses have been proved superior also by trials conducted independently by ten gardeners in different regions of the prefecture: the average index-numbers of yield of the ten trials were 190 for Sironasu×Sinkuro and 167 for Kintyaku×Sinkuro, when 100 was for the yield of the universal variety in each of the regions.

The SAITAMA AGRICULTURAL EXPERIMENT STATION is now yearly furnishing gardeners in the prefecture with F_1 seed of these two crosses of an amount to be used for the commercial culture of a total of about one hundred acres. Besides this, a certain amount of seed of the same crosses is raised by some advanced gardeners in the prefecture who have been supplied with our stock seeds of the parental varieties, and the crossed seed is distributed yearly to other prefectures of the country by certain commercial seed dealers.

TABLE 16

Comparative yields per 100 square meters in a four-years trial of the crosses Sironasu×Sinkuro and Kintyaku×Sinkuro with the variety Sinkuro (in kilograms).

YEAR	SINKURO	SIRONASU × SINKURO	KINTYAKU × SINKURO
1923	131.56	461.84	363.15
1924	186.69	364.46	303.52
1925	525.37	738.00	686.08
1926	330.45	498.15	418.20
Average	293.52	515.61	442.74
Percentage	100	175.7	150.8

THE TECHNIQUE OF CROSS-POLLINATION

The author (1924) reported the flowering habit and the mechanism of flowers of the egg-plant. The first flower appears on the seventh to thirteenth internode of the main stem. Some nodes below the first flower, as a rule, produce branches; the farther up the position of the node the greater is the vigor of the branch from that node.

It is desirable that all branches except the upper one or two be cut off, since lower ones will bear only poor seed-fruits. The first flower on the main stem is also better cut off, as it does not promise a rich seed-fruit and if it produces fruit, it is liable to make the growth of the plant poorer. Thus, the second flower on the main stem and the first flowers on the branches are most suitable for crossing. If these flowers can not be used owing to some reasons such as an insect injury, failure to pollinate due to long-continued rains, etc., the next flowers on the same stem and branches may be employed. Flowers later than these do not usually produce vigorous seed.

One or two days before flowering, the flower bud is quite large and easily emasculated. With a small pair of forceps, the stamens surrounding a pistil are seized and pulled out. The emasculated flower is wrapped in a

small piece of transparent paraffined or parchment paper, which allows the flower to be observed and facilitates pollination, and the piece of paper is secured in position with a pin. The use of a small bag instead of a paper piece is less favorable, because the flower bud is directed obliquely downwards and so that, when it rains, water is apt to stand in the bag. The flower bud for pollen is also wrapped in a piece of the same paper.

The stigma matures as soon as the flower opens, and is receptive for a period of two or three days in general. The anther dehisces at a terminal pore soon after the flower has opened, but, when the flower is wrapped in a piece of paper in the manner as described above, the better part of pollen is preserved in the anther and remains capable of functioning for about three days longer.

When the emasculated flower is seen through the paper wrapper to have opened, pollination is made. Pollen is obtained satisfactorily by slitting one side of an anther with the tip of a small pair of forceps in such a way that the pollen is scraped out on the tip. The amount of pollen obtained from one side of an anther is enough to pollinate one flower. The pollinated flower is wrapped again in paper, and is marked as pollinated. Flowers thus treated give 80 to 90 percent of successful crosses.

SUMMARY

1. The writer has made a comparison between forty-one intervarietal crosses of egg-plants and their parents.

2. In most crosses the F_1 seed was heavier as the immediate effect of cross-pollination than the selfed seed of the mother plant. The increase in weight varied widely, averaging 11.8 percent, and the highest increase was 71 percent over the selfed seed of the mother plant.

3. There was a positive correlation, though not large, between the increase in weight of F_1 seed and the weight of seed of the pollen parent.

4. The wide variation in the increase in weight of the F_1 seed is regarded as due to the difference in heterozygosity of the growth factors of the embryo, as well as to the difference of the capability of the pericarp to the increase in size of the embryo.

5. In the stem-diameter, the cross averaged 5.8 percent thicker than the average of both parents and almost equal to the thicker parent. The increase in the thickness, however, varied widely, and the highest one was 22 percent over the thicker parent.

6. The increase in plant-height of the cross displayed a very similar state as in the case of the stem-diameter. The cross averaged 6.4 percent taller than the average of both parents and almost equal to the taller

parent. The highest increase in height was 18 percent over the taller parent.

7. Either in the stem-diameter or in the plant-height, the variation in the rate of increase or decrease of the cross from the thicker or taller parent agreed well with the distribution of the normal curve. It is, however, reasonable enough to be considered that the variation is not attributed to a simple fluctuation but is concerned with the difference in heterozygosity.

8. The increase in the stem-diameter and that in the plant-height of the cross had a tendency to associate mutually, though the association was not very close.

9. The first-harvesting time was earlier in most crosses than that of the parents, although it ranged so widely that a cross was 5 days earlier than the early parent while another was 4 days later than the late parent. In average it inclined 83.7 percent from the late parent towards the early parent and 16.3 percent from the early parent towards the late one.

10. A greater number of crosses yielded more even than the better parent. The cross exceeded in yield the better parent by 17.0 percent on the average, and a cross which showed the highest increase yielded 140.8 percent more than the better parent.

11. There was a close positive relation between the yield of the parents and that of the cross.

12. There was no appreciable relation between the yield of the parents and the increase in yield of the cross.

13. There was found apparently no relation between the difference in yield of both parents and the increase in yield of the cross.

14. Most of the crosses which exhibited marked increases in yield were given by varieties of widely diverse types.

15. There was a tendency for the crosses which gave greater increases in yield to show greater degrees of hastening in the time of production.

16. F_1 expressions of certain other characters have been briefly described.

17. Two crosses were determined as the most superior ones for practical use, and they have come to be grown for commercial culture to some extent in Japan.

18. Finally, the technique of crossing egg-plants has been described.

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LINKAGE STUDIES IN *PHARBITIS NIL*. I.

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INTRODUCTION

In *Pharbitis Nil*, the Japanese morning glory, 10 linkage groups have been detected, including 34 genes (IMAI 1929). Further studies show that the rayed linkage group is absorbed into the contracted group and a new retracted group is established. Therefore, we have still 10 linkage groups in this plant, but containing 50 loci instead of the previous 34. In this paper the writer attempts to present only new linkage data which do not overlap those given in the previous report. For a description of the characters the reader is referred to the writer's register note (IMAI in press). To save space various tables showing independent segregation are omitted.

VARIEGATED LINKAGE GROUP

Four genes, variegated (v), crumpled-1 (c_1), Blown-1 (B_1) and fasciated-3 (f_3), were found to be included in the variegated linkage group. The recombination percent was 17.7 for v and c_1, 29.3 for v and B_1, and roughly 20–25 for v and f_3. Further experiments bring in 4 genes which are found to be grouped with them. On selfing F_1 obtained by crossing variegated with brown (b_r), the writer recorded F_2 as shown in table 1.

The data show linkage between variegated and brown; therefore brown is considered to be included in this linkage group. This fact is still further

TABLE 1

F_2 from the cross of variegated by brown.

CROSS	+	v	b_r	v b_r	TOTAL
401×405	45	19	11	0	75
402×405	46	17	23	0	86
Total	91	36	34	0	161

substantiated by the additional linkage data between crumpled-1 and brown. From crosses between crumpled-1 and brown, the writer obtained F_2 as indicated in table 2.

TABLE 2

F_2 from the cross of crumpled-1 by brown.

CROSS	+	c_1	b_r	c_1 b_r	TOTAL
401×405	48	16	11	0	75
402×405	40	23	23	0	86
Total	88	39	34	0	161

Feathered is a character recessive to normal, and even (e_v) acts as a modifier for feathered. A cross was made between 2 "parental stocks"; 1, variegated and heterozygous for feathered, the other, heterozygous for deformed (d_e). Among a number of F_2 families, 3 gave practically the same results, showing segregation for variegated, feathered, even and deformed, as shown collectively in table 3.

TABLE 3

F_2 showing linkage between variegated and even.

CROSS	+	v	f_e	f_e v	e_v	e_v v	d_e	d_e v	TOTAL
189s×215s	180	58	42	12	15	0	45	10	263

Of the segregating genes, feathered was known to be included in the cordate linkage group, and deformed is found to be linked with yellow, which constitutes, together with the other genes, the yellow linkage group. Therefore the 3 genes, variegated, feathered and deformed, segregate independently of each other in simultaneous assortment. Even acts as a modifying character to feathered. The segregating ratio is expected to be 36 normal ($27{+}{+}{+}$; $9{+}e_v{+}$): 9 feathered ($9\ f_e{+}{+}$): 3 even ($3\ f_e\ e_v{+}$): 16 deformed ($9{+}{+}d_e$; $3f_e{+}d_e$; $3{+}e_v\ d_e$; $1\ f_e\ e_v\ d_e$). The deficit of deformed in table 3 is due to its low viability. Among a total of 362, 15 were even and none of them were variegated. This shows linkage be-

tween variegated and even. Therefore, the variegated linkage group is increased by 1 more gene, namely, even.

Faded (f_d) may be included as an additional member to this group from the data in table 4, which is an F_2 obtained by crossing variegated faded with normal.

TABLE 4

F_2 from the cross of variegated faded by normal.

CROSS	+	v	*fa*	v *fa*	TOTAL	χ^2_3
410×415	47	8	11	9	75	(28)
N×VF	75	15	13	11	114	..
26×CT	65	13	12	11	101	..
Total	187	36	36	31	290	..

The recombination frequency is calculated as 31.0 percent. The relation of faded to the other members of this linkage group is not yet known, so we cannot decide the locus in the linear arrangement.

In addition to the above data, the writer obtained another dependent segregation for variegated and couple (c_u), as indicated in table 5.

TABLE 5

F_2 from the cross of variegated by couple.

CROSS	+	v	c_u	v c_u	TOTAL
420×34	180	68	67	10	325

The frequency of recombination for variegated and couple is 37.7 percent. In F_2 of the other cross of crumpled-1 (No. 420) and couple (No. 425), the writer obtained data for crumpled-1 and couple, giving a practically free segregation of 202 normal, 60 crumpled-1, 61 couple and 22 crumpled-1 couple among a total of 345. This fact shows that variegated is present between crumpled-1 and couple.

CORDATE LINKAGE GROUP

This group was known to include 3 genes, cordate (c_o), feathered (f_e) and semi-contracted (s_c). The percentage of recombination was 1.2 for c_o and f_e, 18.6 for s_c and c_o, and 17.7 for f_e and s_c. Therefore, the linear arrangement of these genes on the cordate chromosome is probably c_o—f_e—s_c, with a distance of 1.2 between c_o and f_e, and 17.7 between f_e and s_c. Further data furnish 3 additional genes as members of this group. In F_2, obtained by crossing cordate with precocious (p_c), the writer recorded the linkage data presented in table 6.

TABLE 6

F_2 from the cross of cordate by precocious.

CROSS	+	c_o	p_c	c_o p_c	TOTAL
410×190	179	79	84	5	347

The frequency of recombination is 24.6 percent. The relation of p_c to s_c being not yet determined, we cannot decide whether p_c is located at the left of c_o or at the right of s_c. Two genes, crêpe (c_p) and palmate (p_l), are found to be linked with each other, and also with precocious. In table 7 the F_2 data show repulsion for p_c and p_l.

TABLE 7

F_2 from the cross of precocious by palmate.

CROSS	+	p_c	p_l	p_c p_l	TOTAL
297×929	105	45	46	5	201

The recombination percent is 31.3. The linkage of palmate with crêpe, is shown by the data in table 8.

TABLE 8

F_2 from the cross of palmate crêpe by normal.

CROSS	+	p_l	c_p	p_l c_p	TOTAL
297×929	123	30	27	21	201

The recombination frequency due to crossing over is estimated to be 34.6 percent. With the proofs that p_c is linked with p_l and that p_l is linked with c_p, we expect a dependent relation between p_c and c_p. Actually the segregation shows linkage between them, as can be seen by inspecting the data in table 9.

TABLE 9

F_2 from the cross of precocious by crêpe.

CROSS	+	p_c	c_p	p_c c_p	TOTAL
297×929	110	43	41	7	201

The frequency of recombination is 38.8 percent. With the recombination percent of 31.3 for p_c and p_l, 34.6 for p_l and c_p, and 38.8 for p_c and c_p, the arrangement of the 3 genes in cordate chromosome is probably p_c—p_l—c_p, but we cannot decide definitely without further proof. Cordate shows sometimes a very weak linkage with c_p (IMAI 1924) and, sometimes, practically independent segregation. Among the 3 genes above presented,

p_c, therefore, may be located nearest to c_o. Owing to insufficient information on relation of these 3 linked genes, precocious, palmate and crêpe, to the other previously known linked genes, cordate, feathered and semi-contracted, we cannot arrange their loci beyond the facts described above and in the previous paper.

The proof of independent segregation of the genes included in the cordate linkage group in relation to those included in the variegated group is as follows. Cordate to v, c_1 and B_1; f_e to v and B_1; s_c to v and c_1; p_c to c_1: $c_p{}^r$ (reversed, allelomorphic to c_p) to v, c_1 and B_1.

YELLOW LINKAGE GROUP

The yellow linkage group was noted as including 2 genes, yellow (y) and dusky (d_y), the recombination frequency being 1.0 percent. The later experiments add 3 genes, light (l_t), deformed (d_e) and speckled-reduced (s_p-r), to this group. Light dilutes the flower color, acting on intense. In F_2 from the cross of light with dusky the writer obtained the data showing linked segregation for dusky and light, as shown in table 10.

TABLE 10

F_2 from the cross of dusky by light.

CROSS	+	d_y	l_t	$d_y\, l_t$	TOTAL
421×430	93	45	32	0	170
422×435	94	45	34	0	173
Total	187	90	66	0	343

The same crosses were also segregated for yellow or yellow-inconstant (y^i), the latter being recessive to normal but dominant to yellow, and constituting triple allelomorphs with normal and yellow (IMAI 1930b). The relation between yellow and dusky in these crosses shows close linkage as expected and will not be cited here. In table 11 are shown the F_2 data for light and yellow or yellow-inconstant.

TABLE 11

a. F_2 from the cross of yellow by yellow-inconstant light.

CROSS	y^i	y	$y^i\, l_t$	$y\, l_t$	TOTAL
421×430	93	55	31	1	170

b. F_2 from the cross of yellow-inconstant by light.

CROSS	+	y^i	l_t	$y^i\, l_t$	TOTAL
422×435	94	45	34	0	173

The data indicate considerable closeness of the 2 loci yellow and light. Owing to repulsion in these crosses and the data not being sufficient, the calculation of the recombination frequency is not of much importance, since it does not give a reliable figure. Now it is quite evident that the light locus is situated rather near to those of dusky and yellow.

TABLE 12

Some of F_2 from the cross of yellow by normal heterozygous for deformed.

FAMILY NO.	+	y	d_r	$y\ d_r$	TOTAL
1	225	101	71	2	399
5	23	10	5	1	39
6	91	52	29	0	172
8	92	54	23	0	169
Total	431	217	128	3	779

The linkage data for deformed were furnished by the other F_2 (table 12). Owing to the low viability of deformed there was a deficiency of its segregates. The deformed plants were 128 not-yellow and 3 yellow, on the basis of which figures the recombination frequency is about 15 percent. The writer also obtained coupling data proving linkage between yellow and deformed, but the data were meagre in number and will not be cited.

Speckled-reduced is a modifying gene for speckled and is linked with yellow. The data furnishing linkage between yellow and speckled-reduced are shown in table 13.

TABLE 13

F_2 from the cross of yellow (speckled) by speckled-reduced (speckled).

CROSS	+	y	s_p-r	$y\ s_p$-r	TOTAL
410×440	52	28	26	1	107
410×445	72	23	31	4	130
Total	124	51	57	5	237

The percent of recombination is 28.5. This indicates that speckled-reduced is located farther from yellow than deformed is. The relation of speckled-reduced to the other genes of this linkage group is not yet known.

The independent relations of the genes of the yellow group to those of the variegated and cordate groups are as follows: For the former, y or y^i to v, c_1, B_1, f_d and c_u; d_y to v, c_1, B_1, f_d and c_u; l_t to v and c_u; s_p-r to c_1. For the latter (the cordate group), y or y^i to c_o, f_e, s_c and c_p; d_y to c_o, s_c and c_p; l_t to s_c and c_p; s_p-r to c_o, p_c and c_p.

ACUMINATE LINKAGE GROUP

Three genes, acuminate (a_c), Margined-2 (M_{r2}) and magenta (m_g), were known for the acuminate linkage group. The percentage of recombination was about 0.5 for a_c and M_{r2}, and 21.2 for a_c and m_g. No linked genes have been detected to add new data. The independent relation in segregation is observed in the following cases. For the variegated linkage group, a_c to B_1, f_d and c_u; m_g to v, c_1, B_1, f_d^s (smeary, allelomorphic to f_d) and c_u. For the cordate group, a_c to c_o, s_c and c_p; m_g to c_o, s_c and c_p (c_p^r). For the yellow group, a_c to y (y^s) and d_y; m_g to y and d_y.

CONTRACTED LINKAGE GROUP

From the results of the former experiments the writer reached the conclusion that the contracted linkage group contains 8 genes, interaxil-green, contracted, Margined-1, tube-white, intense, Margined-reduced, white-2 and dragonfly. It was, however, an error to put the 2 genes, white-2 and dragonfly, in this group. The gene for the intensity of the flower color, being linked with white-2, is not intense as previously described, but Dilute. So the two genes, white-2 and dragonfly, must be joined to the duplicated linkage group and excluded from the contracted group. HAGIWARA (1922) considered that dragonfly is weakly linked with contracted and Margined-1, but according to the writer's new data the relations are quite independent. In the previous paper, the writer arranged the genes, excluding w_2 and d_g, in the following order in the chromosome: i_g—c_t—M_{r1}—t_w—i, putting the locus of i_g at 0, of c_t at 5.5, of M_{r1} at 6.5, of t_w at 13.6, of i at 38.2, and of M_r-r at 38.2 ± 3.0.

The later experiments show that the group formerly called rayed is to be combined with this group, and 3 new genes are also included therein. In all, the contracted linkage group contains 11 genes which are interaxil-green (i_g), contracted (c_t), Margined-1 (M_{r1}), tube-white (t_w), intense (i), Margined-reduced (M_r-r), Rayed (R_y), cream (c_r), shrubby (s_h), duskish (d_h) and purple (p_r).

In F_2 of crossing interaxil-green by Rayed the data show linkage between interaxil-green and Rayed, as indicated in table 14.

TABLE 14

F_2 from the cross of interaxil-green by Rayed.

CROSS	R_y	+	i_g R_y	i_g	TOTAL	w_1
470×450	75	6	4	25	110	(34)
471×450	32	5	1	8	46	(21)
Total	107	11	5	33	156	(55)

The percentage of recombination is 10.3. Tube-white was known to be located at a distance of 13.6 units from i_g. If R_y is located to the right of i_g there must be very close linkage between t_w and R_y. Actually, however, this was not the case, but weakly dependent segregation was recorded, as is shown by the data in table 15.

TABLE 15

F_2 from the cross of tube-white by Rayed.

CROSS	R_y	+	$t_w R_y$	t_w	TOTAL
475×450	150	41	40	19	250

The frequency of recombination for tube-white and Rayed is 42.5 percent. This shows that the locus of Rayed is situated to the left of i_g at a distance of about 10.3 units, and yet the figure thus obtained by adding 10.3 to 13.6 differs greatly from 42.5. As formerly stated, cream is linked closely with R_y, the recombination frequency being about 1.2 percent. Therefore cream is located either to the left or to the right at about 1.2 units distance from R_y, which is situated at roughly 10.3 units to the left of i_g.

Shrubby is a mutant character newly found (IMAI in press). The shrubby mutants occurred in one of the F_2 families obtained from a cross, and the data showed linked segregation of shrubby with interaxil-green

TABLE 16

F_2 showing linkage between interaxil-green and shrubby.

CROSS	+	i_g	s_h	$i_g s_h$	TOTAL
471×450	51	5	0	14	67

and Rayed. In table 16 is shown the relation between interaxil-green and shrubby.

The recombination percent is 3.1. The numerical relation in segregation of Rayed and shrubby is shown in table 17.

TABLE 17

F_2 showing linkage between Rayed and shrubby.

CROSS	R_y	+	$R_y s_h$	s_h	TOTAL	χ^2_1
471×450	32	4	1	9	46	(21)

The calculation shows that the recombination percentage for Rayed and shrubby is about 11.0. These data indicate that the s_h locus is situated either to the right or to the left of i_g at about 3.1 units. Beyond this we

cannot fix the locus of shrubby on the contracted chromosome, because the data on which the calculations were made are not sufficient. With these data together we may construct a preliminary chromosome map in the relations as follows: $R_y(0)$, $c_r(\pm 1.2)$, $i_g(10.3)$, $s_h(10.3 \pm 3.1)$, $ct(15.8)$, $M_{r1}(16.8)$, $tw(23.9)$, $i(48.5)$, M_r-$r(48.5 \pm 3.0)$.

Duskish is also found to be included in this group. Table 18 shows the data indicating linkage between shrubby and duskish.

TABLE 18

F_2 showing linkage between shrubby and duskish.

CROSS	+	s_h	d_k	$s_h\ d_k$	TOTAL	χ^2
471×450	28	10	8	0	46	(21)

Although the number observed is very small, it may indicate linkage between the two characters. Duskish gives linkage to tube-white, as indicated in table 19.

TABLE 19

F_2 from the cross of tube-white by duskish.

CROSS	+	t_w	d_k	$t_w\ d_k$	TOTAL
475×450	135	52	56	7	250

The recombination percent is 34.9. The segregation of intense and duskish also shows weak linkage, as is indicated in table 20.

TABLE 20

F_2 from the cross of intense duskish by normal.

CROSS	+	i	d_k	$i\ d_k$	TOTAL	w_1
470×426	72	14	12	10	108	(41)

The recombination frequency is 32.0 percent. The other data, however, show practically independent segregation of duskish to interaxil-green and Rayed. Considering all these data together we presume that the d_k locus is probably situated in the right part of the chromosome.

Purple is another gene which may be included in this group. The data show that the purple locus is probably in the right part of the chromosome, because of linkage with tube-white and duskish, but of practically independent segregation to Rayed and contracted. The data showing linkage, however, being complicated by the simultaneous segregation of other genes, will not be cited.

The proofs for the independency in segregation of the genes of this group in their relations to those of the other groups have been obtained

in the following cases: For the variegated group, i_g to c_1; c_t (c_t^s, star; allelomorphic to c_t) to v, c_1, B_1 and f_d; Mr_1 to v and c_1; l_w to v; i to v, c_1 and B_1; m_r-r^s (margined-slight, allelomorphic to M_r-r) to v; d_k to v and c_1; p_r to v, c_1 and c_w; R_y to f_d. For the cordate group, i_g to c_o, p_c, p_l and c_p; c_t (c_t^s) to c_o, f_e, s_c, p_c and c_p; M_{r1} to c_o and s_c; l_w to c_o and $c_p{}^r$; i to c_o and c_p ($c_p{}^r$); m_r-r^s to c_o; d_k to c_o, s_c and c_p; p_r to s_c and c_p. For the yellow group, i_g to y; c_t (c_t^s) to y, d_k and s_p-r; Mr_1 to y^i and d_y; i to y and d_y; d_k to y and d_y; p_r to y (y^i), d_y and l_t; R_y to y. For the acuminate group, i_g to m_g; c_t to a_c and m_g; M_{r1} to m_g and M_{r2}; l_w to m_g; i to m_g; d_k to a_c and m_g; p_r to a_c and m_g; R_y to a_c.

SPECKLED LINKAGE GROUP

The speckled linkage group was known to include 3 genes, speckled (s_p), white-1 (w_1) and Margined-fluctuated (M_r-f). The former 2, s_p and w_1, are linked very closely with about 0.8 percent of recombination, and w_1 is linked with M_r-f, giving a recombination frequency of roughly 20 percent. No new genes have been detected for this group.

For the proofs of independency of the genes of this group in relation to those of the other groups the writer obtained the following cases: For the variegated group, s_p to v, c_1 and f_d (f_d^s); w_1 to v and c_1. For the cordate group, s_p to c_o, p_c and c_p; w_1 to s_c and $c_p{}^r$. For the yellow group, s_p to y and s_p-r; w_1 to y. For the acuminate group, w_1 to m_g. For the contracted group, s_p to i_g, c_t, M_{r1}, d_k and R_y; w_1 to i_g, c_t, M_{r1}, i, d_k, p_r and R_y.

DELICATE LINKAGE GROUP

For the delicate linkage group two genes, delicate (d_l) and crumpled-2 (c_2), were known, and no new genes which belong to this group have been detected since. The recombination frequency for delicate and crumpled-2 is roughly 5 percent.

The proofs for the independent segregation of delicate to the genes of the other linkage groups previously mentioned are as follows: To v and B_1 of the variegated group; c_o and $c_p{}^r$ of the cordate group; y of the yellow group; a_c and m_g of the acuminate group; l_w, i, d_k, p_r, m_r-r^s and R_y of the contracted group. No data have been obtained for the relation to the genes of the speckled group. Crumpled-2 being linked very closely with d_l, the genes above cited may be independent in segregation, but no accurate data on these relations have been obtained as yet.

PEAR LINKAGE GROUP

The pear linkage group was found to contain four genes, pear (p), fasciated-1 (f_1), fasciated-2 (f_2) and Blown-2 (B_2). The recombination

frequency is roughly 20–25 percent for f_1 and f_2, about 2.5 percent for p and f_1, and 23.5 percent for p and B_2. No new genes have been discovered for this group.

The writer has at hand proofs of the independence of the gene p, in its relations to the genes of the various groups, as follows: For the variegated group, to v, c_1 and B_1; for the cordate group, to c_o and c_p ($c_p{}^r$); for the yellow group, to y; for the acuminate group, to a_c and m_g; for the contracted group, to c_t, t_w, i, m_r-r^s, d_k and R_y; for the speckled group, to s_p and w_1; for the delicate group, to d_l.

DUPLICATED LINKAGE GROUP

The duplicated linkage group was known to include three genes, duplicated (d_p), striped (s_t) and Dilute (D). The recombination percent is 13.7 for d_p and s_t, 25.6 for d_p and D, and 10.1 for s_t and D. Therefore, the order in the chromosome is d_p—s_t—D, with an interval of 13.7 between d_p and s_t, and 10.1 between s_t and D. As was stated in a former section, the two genes, white-2 (w_2) and dragonfly (d_g), should be really included in this group. According to the writer's calculation on the basis of MIYAZAWA's data the recombination frequency for D and w_2 is less than 1.4 percent (IMAI 1921). The writer also obtained the data showing repulsion of high degree between the two genes as shown in table 21.

TABLE 21

F_2 showing repulsion between Dilute and white-2.

CROSS	D	+	t_g	w_1	TOTAL	w_2
455×480	52	21	29	37	139	
460×481	38	21	16	23	98	(26)
Total	90	42	45	60	237	

The results are very close to 6 Dilute: 3 normal: 3 tinged: 4 white-2, which ratio is calculated on the assumption of complete repulsion between Dilute and white-2.

The recombination percentage for w_1 and d_g was estimated to be 25.7 on the basis of HAGIWARA's data (IMAI 1929). As is stated elsewhere (IMAI 1930a), the writer observed great deficit of dragonfly segregating in the hybrid progeny, and it prevented him from fixing the recombination frequency for white-2 and dragonfly in his own data. Quite recently, however, he bred two F_2 families, in which occurred no deficit of dragonfly, with simultaneous segregation of white-2, as shown by the data in table 22.

TABLE 22

F_2 from the cross of white-2 dragonfly by normal.

CROSS	+	w_1	d_g	$w_1 d_g$	TOTAL
420×34	207	36	33	49	325
N×WK	320	50	51	74	495
Total	527	86	84	123	820

The recombination frequency is 23.3 percent. According to fragmental data dragonfly is segregated almost independently in relation to duplicated. The order of the genes above cited on the chromosome may be d_p—s_t—$D \pm w_2$—d_g, with an interval of 13.7 between d_p and s_t, 10.1 between s_t and D, and 23.3 between w_2 and d_g.

Extended (e) is found to be linked with dragonfly, as shown by the data in table 23.

TABLE 23

F_2 from the cross of dragonfly by extended.

CROSS	+	d_g	e	$d_g e$	TOTAL
427×465	108	49	44	9	210

The recombination percentage is 38.3. The relation of extended to the other members of this group, however, is not yet known.

The data in regard to the independence of relations have been gathered as follows: For the variegated group, d_p to v, c_1 and f_d; D to c_1; w_2 to v, c_1, f_d and c_u; d_g to v, c_1 and c_u; e to v and c_1. For the cordate group, d_p to c_o and f_c; w_2 to c_o, f_c, s_c, p_c and c_p; d_g to c_o, f_c, s_c and c_p; e to $c_p{}^r$. For the yellow group, d_p to y; D to y and d_y; d_g to y; e to y. For the acuminate group, D to m_g; w_2 to a_c and m_g; d_g to a_c and m_g. For the contracted group, d_p to i_g, c_t, M_{r1}, i and d_k; D to i; w_2 to c_t, M_{r1}, i, d_k and R_y; d_g to c_t ($c_t{}^s$), Mr_1 and d_k; e to i and d_k. For the speckled group, d_p to s_p; w_2 to s_p and w_1; d_g to w_1; e to w_1. For the delicate group, d_p to d_1. For the pear group, w_2 to p; e to p.

RETRACTED LINKAGE GROUP

Retracted (r) is transmitted independently with respect to the following genes: v, c_1, B_1 and f_d of the variegated group; c_o of the cordate group; y and s_p-r of the yellow group; m_g of the acuminate group; c_t ($c_t{}^s$), M_{r1}, t_w, d_k and R_y of the contracted group; s_p and w_1 of the speckled group; d_1 of the delicate group; p of the pear group; d_p, w_2 and d_g of the duplicated group. These data show retracted not to be included in the linkage groups above mentioned, but in a different group.

Foliate (f_o), a recessive modifier of terminal (t), is found to be linked very closely with retracted, as indicated by the data in table 24.

Therefore the retracted linkage group contains the two genes, retracted and foliate.

TABLE 24

F_2 from the cross of retracted (foliate) by terminal.

CROSS	+	r	t	f_o	rt	rf_o	TOTAL
461×415	86	34	28	0	0	13	161

MISCELLANEOUS

Besides the ten linkage groups above represented, a gene is found which seems to be independent to them, and may be included in another group. Some other genes have been proved to be independent of the genes of some linkage groups, but their relations to the other groups have not been studied as yet. As regards such genes the extent of the proof of independence by experiments is as follows: Maple or m^w (willow, allelomorphic to m) to v, c_1 and B_1 of the variegated group; c_o, f_c, s_c and c_p ($c_p{}^r$) of the cordate group; y and d_y of the yellow group; a_c and m_g of the acuminate group; i_g, c_t, t_w, i, m_r-r^s and d_k of the contracted group; s_p and w_1 of the speckled group; d_l of the delicate group; p of the pear group; d_p, w_2 and d_g of the duplicated group; r of the retracted group. Polymorphic to v, c_1 and B_1 of the variegated group; c_o, s_c and c_p of the cordate group; y and d_y of the yellow group; a_c of the acuminate group; c_t of the contracted group; d_l of the delicate group; p of the pear group; w_2 and d_g of the duplicated group; r of the retracted group; and m of group yet undetermined. White-3 to v, c_1 and f_d of the variegated group; c_o, s_c and c_p of the cordate group; M_{r2} of the acuminate group; M_{r1} and d_k of the contracted group; w_1 of the speckled group; D, w_2 and d_g of the duplicated group; r of the retracted group; and m and M_r-s (Margined-suppressed). Buff to v of the variegated group; $c_p{}^r$ of the cordate group; i of the contracted group; w_1 of the speckled group; p of the pear group; w_2 and e of the duplicated group; and w_3. Crisscrossed to c_1 and $f_d{}^s$ of the variegated group; c_o and $c_p{}^r$ of the cordate group; c_t, i and t_w of the contracted group; d_l of the delicate group; and m^w. Deficient to c_1 of the variegated group; c_o and c_p of the cordate group; i_g, i and p_r of the contracted group; w_2 of the duplicated group. Terminal to v and c_1 of the variegated group; c_o of the cordate group; d_k of the contracted group; w_1 of the speckled group; w_2 and d_g of the duplicated group; r of the retracted group; and w_3. Glabrous to v and c_1 of the variegated group; m_g of the acuminate group; c_t and

M_{r1} of the contracted group; d_g of the duplicated group; r of the retracted group. Wrinkled to d_y of the yellow group; m_g of the acuminate group; M_{r1} of the contracted group; and g (glabrous). Contorted to c_p of the cordate group; d_y of the yellow group; m_g of the acuminate group; c_t, i, M_{r1} and p_r of the contracted group; w_2 of the duplicated group; r of the retracted group; and m and p_y (polymorphic). Petaloid to v of the variegated group; c_o, f_e, s_c and c_p of the cordate group; y of the yellow group; d_k of the contracted group; w_2 and d_p of the duplicated group; and m. Tinged to c_1 of the variegated group; D and w_2 of the duplicated group. Variegated-reduced to v of the variegated group; s_c of the cordate group; y^i and l_t of the yellow group; M_{r1} of the contracted group; d_g of the duplicated group. Side-reduced to y of the yellow group; c_t of the contracted group; r of the retracted group. Lined to c_1 of the variegated group; d_g of the duplicated group; and f_l (flecked).

CONCLUSION

Almost simultaneously, but independently, three authors fixed the chromosome number of *Pharbitis Nil* (YASUI 1928, NAGAO 1928, KANÔ 1929). The haploid number was found to be 15. According to the writer's investigation, ten linkage groups have been established. There may be still five other linkage groups not yet represented by discovered cases of linkage. Up to the present time, over one hundred genes have been detected in this plant (IMAI in press). The genes subjected to the linkage analysis are about 70, of which 50 loci are found to be included in the ten linkage groups with the following distributions:

(1) Variegated linkage group. . . . . v, c_1, B_1, f_3, b_r, e_v, $f_d(f_d^s)$, c_w.
(2) Cordate linkage group. . . . . c_o, f_e, s_c, p_c, p_l, $c_p(c_p^r)$.
(3) Yellow linkage group. . . . . $y(y^i)$, d_y, l_t, d_e, s_p-r.
(4) Acuminate linkage group. . . . . a_c, M_{r2}, m_g.
(5) Contracted linkage group. . . . . R_y, c_r, i_g, s_h, c_t, M_{r1}, t_w, i, Mr-r $(m_r$-$r^a)$, d_k, p_r.
(6) Speckled linkage group. . . . . s_p, w_1, M_r-f.
(7) Delicate linkage group. . . . . d_l, c_2.
(8) Pear linkage group. . . . . p, f_1, f_2, B_2.
(9) Duplicated linkage group. . . . . d_p, s_t, D, w_2, d_g, e.
(10) Retracted linkage group. . . . . r, f_o.

The interrelations between these groups have been found to be independent, so far as the writer's investigation is concerned. The proofs seem to be nearly sufficient to regard them as being different linkage

groups related to the different chromosomes, when an independent relation between the speckled and delicate groups is proved.

SUMMARY

1. Ten linkage groups have been established in *Pharbitis Nil*, including 50 loci. So far as the writer's experiments are concerned, the relations between these groups have been found to be independent.

2. The variegated linkage group is composed of eight genes, variegated (v), crumpled-1 (c_1), Blown-1 (B_1), fasciated-3 (f_3), brown (b_r), even (e_v), faded (f_d) and couple (c_u). The frequency of recombination is 17.7 for v and c_1, 29.3 for v and B_1, roughly 20–25 for v and f_3, and about 31.0 for v and f_d. The b_r locus seems to be situated not far from those of v and c_1, and e_v also from that of v. Couple is linked with v; the recombination frequency is about 37.7 percent; and its location on the chromosome may be c_1—v—c_u, or *vice versa*.

3. The cordate linkage group was noted as containing three genes, cordate (c_o), feathered (f_e) and semi-contracted (s_c). The linear arrangement of these genes in the chromosome is probably c_o—f_e—s_c, with a distance of 1.2 between c_o and f_e, and 17.7 between f_e and s_c. Precocious (p_c) is found to be linked with c_o, the recombination percent being about 24.6. The other two genes, palmate (p_l) and crêpe (c_p), are linked with each other with 34.6 percent of recombination, and are also linked with p_c. The recombination frequency is about 31.3 percent for p_c and p_l, and about 38.8 percent for p_c and c_p. Crêpe is located farther than p_c from c_o.

4. The yellow linkage group contains five genes, yellow (y), dusky (d_y), light (l_t), deformed (d_e) and speckled-reduced (s_p-r). The frequency of recombination for y and d_y is 1.0 percent, showing a very short distance between the two loci. Light is linked rather closely with y as well as with d_y. Speckled-reduced is located about 28.5 units from y, and d_e is about 15 units from the same.

5. The acuminate linkage group was known to include three genes, acuminate (a_c), Margined-2 (M_{r2}) and magenta (m_g). The recombination percent is about 0.5 for a_c and M_{r2}, and 21.2 for a_c and m_g. No new genes have been detected for this group.

6. The contracted linkage group includes eleven genes, interaxil-green (i_g), contracted (c_t), Margined-1 (M_{r1}); tube-white (t_w), intense (i), Margined-reduced (M_r-r), shrubby (s_h), Rayed (R_y), cream (c_r), duskish (d_k) and purple (p_r). Experimental data giving rough material make possible the drawing of a preliminary chromosome map of the following

relations: $R_y(0)$, $c_r(\pm 1.2)$, $i_g(10.3)$, $s_h(10.3 \pm 3.1)$, $c_t(15.8)$, $M_{r1}(16.8)$, $t_w(23.9)$, $i(48.5)$, M_r-$r(48.5 \pm 3.0)$. The loci of the two genes, duskish and purple, seem to be in the right part of the chromosome.

7. The speckled linkage group was noted as containing three genes, speckled (s_p), white-1 (w_1), and Margined-fluctuated (M_r-f); the recombination percent is about 0.8 for s_p and w_1, and roughly 20 for w_1 and M_r-f. No genes have been analyzed to add new members for this group.

8. Only two genes, delicate (d_l) and crumpled-2 (c_2), have been found to compose the delicate linkage group. The recombination frequency for d_l and c_2 is roughly 5 percent.

9. The pear linkage group was found to include four genes, pear (p), fasciated-1 (f_1), fasciated-2 (f_2) and Blown-2 (B_2). The recombination percent is roughly 20–25 for f_1 and f_2, about 2.5 for p and f_1, and 23.5 for p and B_2. No new genes have been determined for this group.

10. The duplicated linkage group is composed of six members, duplicated (d_p), striped (s_t), Dilute (D), white-2 (w_2), dragonfly (d_g) and extended (e). The recombination percentage is 13.7 for d_p and s_t, 25.6 for d_p and D, 10.1 for s_t and D, less than 1.4 for D and w_2, 23.3 for w_2 and d_g, and 38.3 for d_g and e. Their order on the chromosome may be d_p—s_t—$D \pm w_2$—d_g, with an interval of 13.7 between d_p and s_t, 10.1 between s_t and D, and 23.3 between w_2 and d_g. Extended is located at a distance of 38.3 units on either the left or the right side of d_g.

11. The retracted linkage group is composed of two genes, retracted (r) and foliate (f_o), the recombination frequency being low.

12. Some other genes, which are independent of those included in the ten linkage groups, are presented.

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INHERITANCE IN THE HOUSE MOUSE, THE LINKAGE RELATIONS OF SHORT-EAR, HAIRLESS, AND NAKED[1]

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[1] Based on a thesis for the degree of Sc. D.

INTRODUCTION

In the years 1926, and 1927, two new unit characters of mice were reported, one a recessive, the other a dominant, both causing absence of hair. The first of these, the recessive Mendelian character, "hairless," was described by BROOKE (1926), being derived from a hairless male and female captured in London. The second, "naked," an incomplete dominant, appeared as a mutation in the mouse stocks of the UNIVERSITY OF LATVIA in Riga and was described and shown to be a Mendelian character by LEBEDINSKY and DAUVART (1927). Through the efforts of Doctor CASTLE mice of these two types were received at the BUSSEY INSTITUTION in the spring of 1928, and during the past year and a half tests have been in progress to detect possible linkage with the other known characters of mice. This paper presents data proving a linkage of the recessive hairless with piebald, and showing the absence of linkage between naked and all of the other well established characters.

New data are also presented on the linkage of short-ear and dilution, together with a study of the multiple effects of the gene causing short-ear, particularly in regard to alterations in the shape of the skull.

The first section of the paper is devoted to a description of the Mendelian or apparently Mendelian characters which have been reported in the house mouse. Known facts concerning linkages are also presented, but, owing to the very complete review of linkage data given by GATES (1926a), less emphasis is put on this than on the discussion of the nature and history of the unit factors. The second section of the paper presents new data gathered by the author. For a more complete bibliography than is here given the reader should consult CUÉNOT'S article (1928).

THE UNIT CHARACTERS OF THE HOUSE MOUSE

Agouti and its allelomorphs

Non-agouti

Non-agouti is the lowest member of the agouti series of allelomorphs, all others being dominant to it. Whereas its allelomorphs suppress the development of pigment in some part or other of the coat, the non-agouti gene permits the maximum development of pigment throughout the length of each hair. Hence when non-agouti is substituted for agouti in a mouse otherwise of the wild gray type the pelage, instead of being gray, is uniform black in color.

Black-and-tan

Black-and-tan mice are similar in appearance to non-agoutis except that the belly is whitish, cream, or bright yellow, with occasionally a

patch of reddish-brown hair between the front legs. As manifested in the light belly, this gene is dominant to all other members of the agouti series, but as manifested in the black back it is recessive to agouti, white-bellied agouti and yellow.

The name was first applied to the darker forms of sable mice which are genetically modified yellows, black-and-tan (as it is now known) not being reported till DUNN (1928) obtained some mice of this type from an English fancier and established the character as an allelomorph in the agouti series.

Black-and-tan has occurred at least once as a mutation in a laboratory stock, PINCUS (1929) having obtained a single black-and-tan mouse in the ninth inbred generation of a non-agouti stock. I have recently found what appear to be four similar mutants in my own crosses. These will be discussed in more detail in a later section of the paper.

Agouti

The agouti gene causes the development of a sub-apical yellow band on each hair, the black and brown pigments being suppressed in this region and only the yellow showing. The result is to make an otherwise black coat into the grayish-brown coat characteristic of the wild house mouse and many other rodents.

White-bellied agouti

White-bellied agouti mice have a typical gray or agouti dorsum, but the belly is whitish or yellow like that of the black-and-tan. They are indistinguishable in appearance from mice heterozygous for black-and-tan and agouti.

LITTLE (1916) has reported four mutations to white-bellied agouti, but unfortunately the nature of the crosses in which they appeared make it impossible to tell whether the mutations were from agouti or from non-agouti.

Owing to the fact that the light belly of white-bellied agouti appears phenotypically as a distinct character rather than as an intermediate form between agouti and yellow, MORGAN (1914) suggested that it is due to a gene different from but closely linked with the agouti gene. However, in a backcross generation of 180 individuals raised to test this hypothesis he failed to obtain a crossover.

Yellow

The yellow factor in the heterozygous condition causes a reduction of black and brown pigment, thus leaving the hair a bright yellow. In the

presence of certain modifying genes, however, yellow mice are changed into "sables" or "black-backed yellows," in which the back is considerably darkened, the most extreme individuals being similar in appearance to black-and-tans. The eyes are always dark pigmented. The gene for yellow also induces a marked accumulation of fat accompanied by a tendency to sterility. In the homozygous condition it is lethal, causing the death of the embryo at or shortly after implantation.

Albinism and its allelomorphs

Albinism

CUÉNOT (1902), CASTLE and ALLEN (1903, ALLEN 1904) showed albinism to be inherited as a Mendelian factor.

It is linked with pink-eye and shaker.

Extreme dilution

Mice homozygous for the extreme dilution factor are practically white in the first pelage, but later acquire a brownish shade on the dorsum. The eyes are only a trifle lighter than those of full colored mice and the ears and scrotum show distinct dark pigmentation. Extreme dilution is incompletely dominant to albinism.

Chinchilla

The chinchilla gene causes a slight dilution of the coat pigments, especially the yellow, and is therefore more conspicuous in agouti than in non-agouti animals as these normally show the most yellow. It is incompletely dominant to extreme dilution and to albinism.

Color

Full color is normally completely dominant to all lower members of the albino series, but under certain conditions the dominance is incomplete. Thus CUÉNOT (1928) states that pink-eyed mice heterozgous for color and albinism or even for color and chinchilla are appreciably lighter than those homozygous for full color, and PLATE (1910) and RABAUD (1919) have reported mice heterozygous for color and albinism (and also for brown and perhaps other factors in the case of PLATE's mice) which developed large patches of white or silvered hair as they grew older. A further demonstration of the incomplete dominance of color has been furnished by HANCE (1927, 1928) who finds that mice carrying albinism, when treated at ten to fourteen days of age with just sufficient X-rays to produce hair falling, regenerate a semi-white coat.

Brown

In brown mice all black pigment is absent, the remaining pigmentation, according to WRIGHT (1917), being "really intermediate between black and yellow, uniformly throughout skin, coat and eye." The result is cinnamon or chocolate colored mice according as the brown factor is combined with agouti or non-agouti.

Brown is usually entirely recessive to its allelomorph, black, but in at least two cases the dominance is partially reversed. Pink-eyed non-agouti mice carrying brown in the heterozygous condition are distinguishable from those homozygous for black by their lighter shade. A more striking lack of dominance is found in combination with silver. When silver mice carry the brown factor in the heterozygous condition the silvering is greatly intensified, the underfur being practically white and the general shade of the pelage little if any darker than that produced by extreme dilution. The eye is black. Chocolate silvers, despite the double dose of the brown factor, are often darker than these heterozygous black mice, though the unsilvered hairs are brown rather than black.

LITTLE (1916) has reported one case of a mutation from black to brown, cinnamon mice appearing in a strain of grays inbred brother with sister for five generations and by other matings for several generations before that.

Pink-eye

The eye of pink-eyed mice, as the name implies, is very light, closely resembling that of albinos; but according to Miss DURHAM (1911) traces of pigment are present in both retina and iris. The color of the skin and coat is also considerably lightened, the pigmentation as reported by WRIGHT (1917) being more or less intermediate between black and yellow.

LITTLE (1916) has reported one case of mutation to pink-eye, mice of this type appearing in a strain previously tested for the absence of the character.

Pink-eye is linked with albinism and shaker.

Dilution

The recessive factor, dilution, produces a general lightening of the coat color, not by a reduction in the number of pigment granules but by causing them to be clumped together. It is ordinarily entirely recessive but in two or perhaps three mice described in detail in a later section of this paper I have obtained what appears to be a temporary reversal of dominance.

Dilution, as first discovered by GATES (1927, 1928a), is very closely linked with short-ear.

Piebald

Piebald is an imperfectly recessive character consisting of white spotting. Most commonly there is one white patch in the belly and one or more white patches on the back and forehead, but according to DUNN (1920) the homozygous piebald genotype "may vary somatically from solid colored to all white with dark eyes."

Mice heterozygous for piebald often show a small white area on the belly. When in addition the gene from black-eyed white is also present in the heterozygous condition, the result is the so-called "variegated" or "Type A" spotting, a type with much more white than that caused by either gene acting alone. Piebald cannot therefore be classified as entirely recessive.

Data presented in a later section of this paper show piebald to be linked with hairless.

Black-eyed white

In the heterozygous condition the gene for black-eyed white produces a low grade of spotting, while in the homozygous condition it is lethal, causing death from anemia shortly before or after birth. According to SO and IMAI (1920) it can be distinguished somatically from piebald by the lack of a sharp line of demarcation between the light and dark areas, the white patches overlapping the dark as "silvering" or occasional white hairs. The name is derived from the fact that when combined with piebald in the homozygous condition it may produce all white mice with black eyes, the so-called "black-eyed white" mice. The black-eyed white gene acting alone produces only small areas of white.

Spotting modifiers

Both types of spotting, but especially piebald, are subject to wide variation with respect to the extent and location of the white areas. CUÉNOT (1928) states it as probable "that spotting is conditioned by multiple or allelomorphic factors for extension whose effect is algebraically additive." He finds that the lower degrees of spotting are dominant over the higher. DUNN (1920) also reports spotting modifiers "which appear to increase the general amount of color forming substance" so that in their presence both black-eyed white and pieblad genes produce relatively less than the normal amount of white spotting.

The first and only successful isolation of pattern varieties was accomplished by DUNN and DURHAM (1925), who, by inbreeding two strains of

piebald, one with a white face and the other a white-belted variety, and then crossing, obtained clear segregation in the F_2. The gene causing white face was shown to be dominant as it appeared in practically all F_1 individuals and in three-fourths of the F_2's. The belted pattern, on the contrary, was recessive.

CUÉNOT (1904) and DUNN and DURHAM (1925) both reach the conclusion that the finest details of piebald spotting are not represented in the germ plasm, but are rather due to variations in the environment.

Silver

Silver is a multiple factor character, though probably with one principal recessive gene involved. It consists of the presence of white hairs scattered throughout the coat, but the number of such hairs and hence the intensity of the silvering may vary through a wide range. In black mice heterozygous for brown it is greatly intensified, the whole underfur being practically white.

Data recently published by KEELER (1930) indicate that the principal gene for silver lies on the same chromosome as the gene for rodless.

Hairless

Hairless is a recently studied recessive character causing reduced viability, partial sterility especially in the females, and practically complete loss of hair after the second week of life (figure 1). The homozygous hairless young are indistinguishable from their normal sibs until about fourteen days of age when, at just about the same time that the eyes open, they can be recognized by loss of hair on the upper eyelid. At the same time, shedding begins on the under jaw and on all four feet just above the toes, and slightly later at the base of the tail. During the course of the next week a wave of shedding spreads from these centers, especially that around the eye, until it has passed over the entire body, leaving the animal completely naked except for a few scattered hairs. The vibrissæ may or may not be present. Sometimes they remain indefinitely, sometimes they are lost as early as the fifteenth day, but they always reappear eventually for in old individuals at least a few are invariably present. At about six weeks of age some slight regeneration of the whole coat occurs, but it is usually so slight as easily to escape notice. One piebald male in my stocks, however, developed sufficient re-growth so that the piebald pattern was distinctly visible. The skin, when naked, is often slightly moist, but usually comparatively smooth, though old animals may show a few criss-cross wrinkles on the head.

The majority of hairless females are entirely sterile, but occasionally one gives birth to a litter. Of the four litters, however, which have been born to hairless females in my stocks, all have been dead when found except for a single individual which was given to a foster mother but died

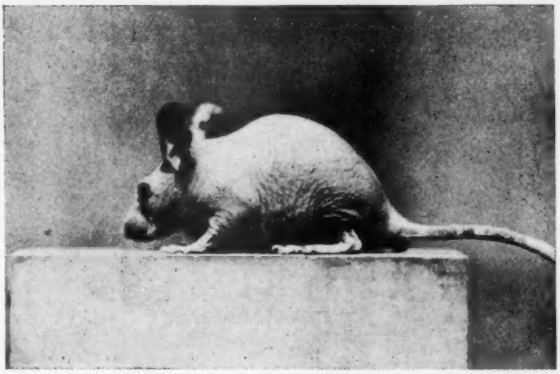


FIGURE 1.—Male homozygous for hairless (h^rh^r).

FIGURE 2.—Male heterozygous for both hairless and naked ($H^rh^rN_n$), showing the goggle-like rings of hair around the eyes characteristic of individuals of this genetic constitution.

soon after. In all cases except this one, death apparently occurred at or very shortly after birth. The males are also considerably reduced in fertility.

The character is entirely recessive except when present in mice heterozygous for dominant hairless or naked. These doubly heterozygous

animals are distinguishable by the increased hairlessness and by the unusual patterns which the hair assumes, especially conspicuous being the goggle-like ring of hair around the eyes (figure 2) often seen in them but never in mice carrying only the gene for naked.

The only reference in the literature to hairless mice which can be stated with complete assurance as applying to mice of the type described above is that of BROOKE (1926) who reports a pair captured in an aviary in London. The hairless mice used by the present author for linkage tests are descended from this pair. Earlier descriptions of hairless mice probably also of this type are given by GASKOIN (1856), MARSHALL (1887), BATESON (1894), ALLEN (1904), POCOCK (1904), and CAMPBELL (1907).[2] All these authors describe the hairless animals as having a skin deeply folded and wrinkled, a characteristic which caused the name "rhinocerous mice" to be applied to them. CAMPBELL gives some data, unfortunately very incomplete, indicating linkage of his "corrugated hairless" with piebald. Were it not for this indication of linkage with piebald, the same linkage as that which I have found, I would suspect from the unusual folding and creasing of the skin reported by all these earlier writers, but not appearing in my own mice, that I was dealing with a different type of hairlessness. It is probable, however, in view of the linkage, that this folded skin is the product merely of environmental conditions or modifying factors, or at most an allelomorph of hairless, but it will certainly be of interest to make a genetic study of hairless mice from new sources on the possibility that other types of hairlessness can be found.

The linkage of hairless with piebald has already been noted, and will be discussed in more detail later.

Naked

Naked is a partially dominant mutation of recent origin. Mice carrying the gene in double dose are completely naked from birth with the exception of occasional hairs hardly visible to the naked eye, even the vibrissæ being absent. They are almost without exception sterile, though young can occasionally be reared from matings of naked males with fully haired females. They seldom attain as much as three-fourths normal size; the body is shrunken, the skin somewhat wrinkled, and the vitality in all respects greatly reduced.

Mice carrying the gene in single dose resemble those homozygous for the recessive hairless character in that the shedding starts in the neighbor-

[2] Another reference to hairless mice is that of BREE, appearing in *Field* for October 5, 1872. p. 328. I have been unable to obtain this reference, and so omit it from the above discussion,

hood of the eyes simultaneously with its opening on about the fourteenth day after birth, and in the course of the following week progresses backwards over the length of the body. Here, however, the similarity ends. In the histological abnormalities of the skin and in the general manner of shedding, there are marked differences between the two types. Unlike mice carrying genes for hairless, those heterozygous for naked can usually be identified prior to the fourteenth day by the shortness and lack of luster of their coat. Unlike them, again, the feet and tail are not centers of shedding; on the contrary, the tail, the fore feet to the elbow, and the hind feet as far as the heel are almost normally haired throughout life. Ears and tip of nose may also maintain a certain amount of covering. Again,

FIGURE 3.—Female heterozygous for naked (N_n).

the shedding in naked mice, instead of consisting of an actual falling of the hair, is the result of the breaking off of the hairs at the surface of the skin, the root remaining for some time. Moreover, the line of demarcation between the naked and haired regions is not so sharp. The most striking difference, however, is the repeated successions of regeneration and shedding exhibited by the heterozygous naked mice. At about one month of age, shortly after the first moult is complete, a new coat begins to appear on the head, the new growth progressing posteriorly over the body, only to be followed by another wave of shedding. This process is repeated throughout the life of the individual at intervals of roughly one month, two or three successive waves sometimes being in evidence at one time as isolated bands of hair across the body (figure 3). The rate of shedding, however, and the resulting coat patterns, vary considerably

from one individual to another. The vibrissae are usually present though they may be of less than normal length and are occasionally absent altogether.

The naked character arose as a mutation in the mouse stocks of the UNIVERSITY of LATVIA in Riga, and was described and shown to be a simple Mendelian dominant by LEBEDINSKY and DAUVART (1927). The only other reference in the literature which clearly applies to mice of this type is GORDON'S (1850) description of three hairless mice sent to him from Elgin. He says of them, "The whole bodies of these three little creatures were completely naked,—as destitute of hair and as fair and smooth as a child's cheek. There was nothing peculiar about the snout, whiskers, ears, lower half of the legs and tail; all of which had hair of the usual length and colour." The presence of hair on the snout, legs, ears, and tail and its absence elsewhere clearly brands these mice as being heterozygous for naked, and probably about one month old.

Short-ear

Short-ear is a recessive character whose primary effect in the homozygous condition is a reduction of the ear to less than one half normal length, but which also causes kinkyness of the tail, changes in shape of the skull, and a slight decrease in size and vigor. The kinky-tail associated with short-ear is easily distinguished from the flexed-tail described by PLATE (1910), and HUNT and PUMAR (1928), by the fact that it is not due to fusion of the vertebrae but rather is purely muscular, disappearing when the animal is etherized. Both GATES (1926a) and KEELER (1927) report rather frequent crossovers between short-ear and kinky-tail,and therefore conclude that the two are due to distinct but linked genes. In extended crosses, however, I have found no evidence that the two can be separated and hence believe them to be expressions of the same gene.

As discovered by GATES (1927), short-ear is very closely linked with dilution, the first crossover to occur having been obtained by the present author (1928). New data on this linkage and on the various effects of the gene for short-ear are given in a later section of this paper.

Rodless

Rodless is a recessive Mendelian character consisting of complete absence of rods and external molecular layer from the eye, and reduction of the external nuclear layer. Usually only one row of nuclei is present, but occasionally three or six rows are found to occur. Rodless mice are totally blind.

KEELER (1930) has reported data indicating linkage of rodless with silver.

Waltzing

Mice homozygous for the waltzing gene are totally deaf and seriously defective in their sense of balance, this inability to orient themselves causing the whirling or waltzing movements for which they are famous. They also show reduced size and viability.

GATES (1926a) has demonstrated that the pure-bred Japanese waltzing mice are descended from *Mus wagneri* rather than *Mus musculus*. GATES (1926b) has also demonstrated in a cross of waltzing and normal mice the first and only case of non-disjunction in mice, the genetic evidence which he presents proving the absence of part of one of the chromosomes carrying the waltzing gene in an F_1 female and half of her offspring. Cytological confirmation of this has been furnished by PAINTER (1927).

Shaker

GATES (1928b) has recently found a new recessive Mendelian character in mice, "shaker," which manifests itself as rapid and continuous up and down movements of the head. The same type of motion is sometimes observed in waltzers but the two factors are entirely distinct. LORD and GATES (1929) find that young shakers are normal in hearing, but that they become deaf at ages ranging from 22 to 29 days. Mice heterozygous for shaker ordinarily possess unimpaired hearing, at least up to 1 year of age, but when waltzing is also present in the heterozygous condition they usually go deaf when from 3 to 6 months old. Shaker is thus incompletely recessive when combined with one dose of waltzing.

Shaker is quite closely linked with albinism, and hence with pink-eye, the meagre data at present available indicating that albinism will lie between shaker and pink-eye on the chromosome map.

Tailless

Tailless is a dominant mutation manifesting itself as a marked reduction or even complete absence of the tail. The homozygous tailless form has never been obtained indicating that it, like yellow and black-eyed white cannot develop to maturity, though embryological evidence of its prenatal death is altogether wanting. In experiments made to test the nature of its inheritance, NÄGELI and LANG (LANG 1912) obtained the expected 1:1 ratio (199 normal to 180 tailless) in a backcross, but a 1:1 rather than a 2:1 ratio in the F_2; and DUBOSCQ (1922) found the charater sometimes

dominant and sometimes recessive. Only DOBROVOLSKAIA-ZAVADSKAIA (1927) obtained the expected Mendelian ratios in all crosses.

No linkage relationships have been determined.

Flexed-tail

Flexed-tail is an imperfect Mendelian character consisting in well marked cases of numerous sharp kinks in the tail due to displacement and partial fusion of successive vertebrae. Several recessive genes are probably involved. It was first reported by PLATE (1910) and BLANK (1916), and what is probably the same character has more recently been reported in this country by HUNT and PUMAR (1928). HUNT finds it to breed true and to give the expected 1:1 ratio in a backcross, though the F_2 ratio is nearer 7:1 than 3:1. PLATE and BLANK obtained even more abnormal results, the character in some cases appearing to behave as a dominant.

Linkage relations have not been determined, but GATES (1926a) believes PLATE'S data to indicate a linkage with pink-eye.

Ectromelus ("Souris Luxees")

An imperfect Mendelian character, ectromelus ("luxee"), consisting of the absence of the tibia from the hind legs and certain malformations of the fibula, was reported by RABAUD (1914). CUÉNOT (1928) interprets the character as probably a simple recessive showing, however, a considerable number of normal overlaps. No linkage tests have been made.

Polydactylism ("hyperdactylie")

RABAUD'S ectromelus mice gave birth to some young showing polydactylism (19 out of 240), one or both hind feet having six or seven toes (RABAUD 1919). Polydactylism, by appropriate crosses, may be separated from the ectromelus form, but the manner of its inheritance is in doubt.

Haemoragic head

Haemoragic head is a semi-lethal recessive abnormality found by LITTLE and BAGG (1924) among the descendants of two different pairs of X-rayed mice. It is highly variable in its expression, consisting in widely varying degrees of malformation of eyes, feet, kidneys, and occasionally other internal organs. In mild cases the eyes may show slight clouding or distortion, or one kidney may be reduced in size; in extreme cases both eyes may be sightless or even lacking and both kidneys entirely absent, this condition causing death about twenty-four hours after birth. Cases

of syndactylism, polydactylism, and especially club feet are occasionally present as expressions of the character, and BAGG (1929) finds that their incidence can be greatly increased by selection. Embryological studies have shown all these defects to be associated with blood extravasations. While the inheritance of haemoragic head is not strictly Mendelian, an excess of normals appearing in all crosses, it is probably the effect of a single recessive gene. BAGG (1925) reports 17 normal overlaps among 179 offspring from matings of affected (hence homozygous) individuals, while F_2 and backcross generations (BAGG and HALTER 1927) gave ratios of normals to abnormals of 1082:282 and 333:240 respectively.

FIGURE 4.—Dwarf mouse and normal sib two months old.

Another type of deformity appearing among offspring of both X-rayed and control mice and named by LITTLE and BAGG (1924) the "Lethal head and jaw abnormality" is now regarded by BAGG as a manifestation of the same gene that causes haemoragic head.

No tests for linkage of haemoragic head with other characters have been reported.

Dwarf

Dwarf is a recessive Mendelian character causing a great reduction in growth rate after the fourteenth day, with the result that mature dwarf mice are scarcely more than one-fourth normal size (figure 4). Up to the fourteenth day growth is practically normal though affected individuals can be identified on about the twelfth day by their shorter noses and tails. The dwarfs are sterile and somewhat reduced in vigor, showing little tendency to jump or run and a marked thinning of the hairs as they get old,

but in other respects their health and viability are good. They were first reported by the author (1929). Linkage tests are now in progress.

Sex-linked lethals

Possible sex-linked lethals have been reported by two investigators. MORGAN (1914) found a ratio of 76 females to 26 males in the offspring of a certain cross, and believes this to indicate a probable sex-linked lethal. LITTLE (1920) obtained a similar excess of females (100 to 53) in a line of Japanese waltzers and attributes it to the same cause. In neither case was it shown that the lethal was transmitted to half the daughters of an affected female, the other half being normal, as should be the case with a sex-linked lethal, and in other respects the data are rather incomplete. It is, of course, impossible to tell whether or not the same gene was involved in the two cases.

Hyperglycaemia

CAMMIDGE and HOWARD (1926) have reported a recessive Mendelian character in mice consisting of an excess concentration of sugar in the blood. Their ratios are very close to the expected. It remains to test this character, hyperglycaemia, for linkage with most of the other known factors, but absence of linkage with albinism is clearly shown by their crosses.

Angora

COCKS (1852) described a long-haired or angora mouse caught in England, but this mutation does not seem to have reappeared.

Congenital eye anomaly

PEARSON (1924) has reported an eye defect, probably congenital, consisting of opacity of the lenses and occasionally reduction in size of the eye, which appeared in about 1.5 percent of a strain of albino mice. The manner of inheritance is in doubt.

Twisted nose

The occurrence of a twisted or stunted nose due to a shortening of one or both of the nasal bones has been reported by KEELER (1929) in four closely related mice. The manner of inheritance suggests a "dominant unit character with normal overlaps," but this must be regarded as uncertain due to the small amount of data.

DISCUSSION OF THE KNOWN UNIT CHARACTERS OF THE HOUSE MOUSE

A comparison of the dates of discovery of the known unit characters in mice shows that those first discovered were nearly all concerned with

coat color, whereas those more recently described are principally anatomical or physiological abnormalities. Of the eight sets of allelomorphs affecting the coat pigmentation, all were known prior to 1900 except silver (a multiple factor character and hence probably the result of long selection), the black-and-tan allelomorph of the agouti series, and extreme dilution and chinchilla in the albino series. While a more intensive search than ever before has been maintained since 1900 for new genes and the total number more than doubled, few of the new characters are concerned with pigmentation. It would therefore seem probable that all or practically all the discoverable factors of this type are now known, and that future search will reveal principally mutations which, like rodless, tailless, or hyperglycaemia, are concerned with function or internal structure.

MORGAN, BRIDGES, and STURTEVANT (1925) point out that "most of the dominant mutations in Drosophila are lethal when homozygous." The same generalization holds in the case of mice, three of the five dominant mutations (yellow, black-eyed white, and tailless) having a recessive lethal effect, while naked is a semi-lethal and only light-belly is without damaging consequences in the homozygous condition. MULLER remarks that this is probably not a peculiarity of dominant genes as contrasted with recessive ones, but because lethal mutations are themselves more common than other kinds and may well be expected to manifest themselves in certain cases in the heterozygote as a visible character.

Whereas mice are like Drosophila in the presence of dominant factors causing death in the homozygous condition, they differ markedly from Drosophila in the almost complete absence of lethals which are apparent only by their lethal effect. MULLER (1928) and others have stated that in Drosophila lethal genes are the most common type. In mice, on the other hand, only two pure lethals (the sex-linked lethals of MORGAN and LITTLE) have been reported, and these are not confirmed by embryological evidence or even well established genetically. It may perhaps be that this is due to lethals being actually less frequent in mice, but it seems more probable that it is the result of the relatively small number of offspring ordinarily raised from a single mating in the case of mice, this making it often impossible to establish the statistically significant difference between 3:1 and 2:1, 1:1 and 2:1, or even 3:1 and 3:0 ratios, necessary to prove the existence of a lethal. That ratios often do show undue departures from the expected is easily seen even by a casual examination of the literature, and I suspect that in some cases at least these departures are due to the action of lethal factors, but to prove this in

TABLE 1

Unit characters of the house mouse with their symbols and linkages.

CHROMOSOME	GENE	SYMBOL	NAME	CROSSOVER PERCENT
1	1	P	Dark-eye	
		p	Pink-eye	
				19.06 in female
	2	C	Full color	13.89 in male
		c^{ch}	Chinchilla	
		c^{d}	Extreme dilution	
		c	Albinism	
				2.5
	3	S^{h}	Non-shaker	
		s^{h}	Shaker	
2	4	A^{y}	Yellow	
		A^{w}	White-bellied agouti	
		A	Agouti	
		a^{t}	Black-and-tan	
		a	Non-agouti	
3	5	B	Black	
		b	Brown	
4	6	D	Density	
		d	Dilution	
				0.06
	7	S^{e}	Normal-ear	
		s^{e}	Short-ear	
5	8	S	Self	
		s	Piebald	
				9.8 in female
	9	H^{r}	Haired	2.6 in male
		h^{r}	Hairless	
6	10	W	Black-eyed white	
		w	Self	
7	11	V	Normal walking	
		v	Waltzing	
8	12	R	Rodded retinae	
		r	Rodless	
				12 ?
	13	S^{l}	Non-silver	
		s^{l}	Silver	
9	14	N	Naked	
		n	Normal coat	
?	15	H	Normal head	
		h	Haemoragic head	
?	16	T	Tailless	
		t	Normal tail	
?	17	D^{w}	Non-dwarf	
		d^{w}	Dwarf	

any given case is a difficult matter. If, however, in mouse crosses the maximum possible number of young is raised from each mating involving heterozygotes, lethal factors if present would ordinarily be revealed. According to GATES (1926a) and KIRKHAM (1920), the production of as many as 75 or 80 young from a pair is not impossible.

While it is both customary and useful to speak of genes as either dominant or recessive, it would seem that in mice many if not most of the genes are, strictly speaking, neither. It is possible to list as incompletely dominant, or incompletely recessive characters, albinism and its allelomorphs, yellow, brown, black-eyed white, shaker, piebald, hairless, naked, tailless, and perhaps dilution. Some of these, for example hairless and albinism, reveal their presence in single dose only under special conditions; and it is not unlikely that by proper experimental methods a number of the other factors would be found also to be detectable in the heterozygous condition.

THE LINKAGE OF SHORT-EAR AND DILUTION

As first discovered and reported by GATES (1927), there exists a remarkably close linkage in the house mouse between the characters short-ear and density and their allelomorphs normal-ear and dilution. To date only one crossover between these two pairs of characters has been reported. GATES (1927, 1928a) has reported the test of 426 individuals of F_2 and later generations from a cross of short-ear and dense with normal-eared and dilute without finding evidence of a single crossover. The present author (1928) has reported the test of 579 individuals from a similar cross. Of this number only one was the carrier of a crossover chromosome. From this single crossover individual was derived a stock of short-eared dilute mice, and a backcross undertaken with a view to obtaining further data on the linkage. From this backcross I have obtained a total of 1034 individuals but no crossovers.

One crossover, however, apparently has been obtained by Miss COPELAND in a backcross generation of 106 individuals. In one litter of seven young, she found a normal-eared dense male along with 4 normal-eared dilute individuals and 2 short-eared dense ones. I have tested this male and find him to be the correct constitution for a crossover, namely, S^eD/s^ed. This is the second crossover to occur between the two loci.

Totalling all data, the number of gametes so far tested is 3150, the number of crossovers 2, and the crossover percent 0.06. These results are summarized in tables 2, 3, and 4.

TABLE 2

Summary of F_2 data from crosses of short-ear×dilute.

	MATING	S^eD	S^ed	s^eD	s^ed	AUTHOR
Observed	$♀\frac{S^ed}{s^eD}\times♂\frac{S^ed}{s^eD}$	827	404	393	0	GATES 1928a
Expected		*812*	*406*	*406*	*0*	
Dev./P.E.		1.1	0.2	1.1		
Observed	Same	1407	722	603	0	SNELL 1928
Expected		*1366*	*683*	*683*	*0*	
Dev./P.E.		2.3	3.5	5.2		

TABLE 3

New data from backcross.

	MATING	S^eD	S^ed	s^eD	s^ed	AUTHOR
	$♀\frac{S^ed}{s^eD}\times♂\frac{s^ed}{s^ed}$	0	481	432	0	SNELL
	Same	1	55	50	0	COPELAND
	$♀\frac{s^ed}{s^ed}\times♂\frac{S^ed}{s^eD}$	0	64	57	0	SNELL
Observed		1	600	539	0	Total
Expected with complete linkage		*0*	*570*	*570*	*0*	
Dev./P.E.			2.6	2.6		

TABLE 4

Summary of data showing linkage of short-ear and dilution.

MATING	NUMBER OF OFFSPRING TESTED	NUMBER OF CHROMOSOMES TESTED	NUMBER OF CROSSOVERS	CROSSOVER PERCENT	AUTHOR
F_2	426	852	0	0	GATES 1928a
F_2	579	1158	1	0.09	SNELL 1928
Backcross	1034	1034	0	0	SNELL
Backcross	106	106	1	0.94	COPELAND
Total	2145	3150	2	0.06	Total

As was suggested to me by Doctor EAST, the two individuals interpreted above as crossovers may also be interpreted as mutants, for a mutation on chromosomes of the constitutions S^ed or s^eD would give chromosomes S^eD or s^ed that would be indistinguishable from those produced

by crossing over. Hence the hypothesis of mutation would satisfactorily account for the observed results. I am inclined, however, to regard the occurrence of a crossover as the more probable explanation. Mutations at the loci for short-ear and dilution have never been known to occur in laboratory stocks, except as already noted, and must be of very rare occurrence. Moreover, to explain the normal-eared dense individual obtained by Miss COPELAND otherwise than as a crossover it would be necessary to postulate a reverse mutation, that is, one from the mutant type back to the normal or wild type, and such mutations have been shown by observations on Drosophila to take place only with great rarity. This fact of the difference of mutation rate in the two directions, while not enabling us to choose finally between the two explanations with the data at present available, would enable us to make a choice were a larger amount of reliable data to be obtained. If an extensive backcross $(S^e d)/(s^e D) \times (s^e d)/(s^e d)$ yielded approximately the same number of double dominant $(S^e D)/(s^e d)$ offspring as of double recessive ones, it would be safe to infer that crossing over rather than mutation was responsible for their production.

In the F_2 generation which I obtained from matings of mice heterozygous for short-ear and dilution there is a significant deficit of short-eared dense individuals as indicated by the Dev./P.E. of 5.2 (table 2). Likewise, in the backcross generation there are less than the expected number of short-eared dense offspring, though here the Dev./P.E. is only 2.5 and hence not surely significant (table 3). These departures from the expected are attributable to lesser viability of short-eared mice as compared with normal-eared ones. All young had to be raised to at least fourteen days before they could be identified and during this period there were numerous deaths in the majority of litters, most of them due to paratyphoid. There is reason to believe that an undue proportion of these deaths were among short-eared dense individuals. Had the conditions for raising the young been more favorable, all ratios would probably have been normal.

REVERSAL OF DOMINANCE OF DILUTION

In the course of the backcross experiment two young were born which were first classified as short-eared dilutes and hence as crossovers, but which it now seems were almost surely short-eared and intense. The first of these, by female 155, lived only about a month, but during this time was examined on three occasions and carefully compared as to coat color with other dilute individuals. On each occasion its coat was unmistakably

dilute, and were it not for the second individual discussed below it would have been classified as a crossover. It was noticeably smaller than the single sib which survived the first week of life, and its hair was slightly thinner than normal.

The second case was a female, one of four young produced by a mating of female 71 to a short-eared dilute male. This female was examined at 17, 23, and 24 days of age, and on each occasion was unmistakably a short-eared dilute cinnamon. Its sibs, two short-eared intense and one long-eared dilute, were killed at the time of the first examination in order that this one might receive the full care of the mother. The next examination was made at 44 days of age and revealed the unexpected fact that the supposed crossover had moulted to a clear cut intense cinnamon. As in the case described just above, the apparently short-eared dilute individual was smaller than its sibs.

In the course of tests for possible linkage of naked with dilute a third case appeared, similar to the above, though not quite so well checked. A naked female, R177, mated to a dilute chocolate male, gave birth to a litter of seven young. These were examined at 10 and 15 days of age and one of the young, female R352, a cinnamon naked, was classified on both occasions as dilute. When the next examination was made, however, this female, then 36 days old, had regenerated a second coat which was clearly intense.

These three cases, of which one was very carefully checked, indicate that under certain conditions mice heterozygous for dilution may appear for about the first month of life as if homozygous dilute, the dominance of the gene for density being temporarily reversed. More cases would be necessary to prove that only individuals carrying dilution and never those homozygous for density can exhibit this phenomenon, but it seems probable that this is the case. It may be added that of the 603 short-eared intense ($s^e s^e DD$) F_2's none were of this pseudo-dilute type; if they had been they would have been classed as crossovers. It is of interest to note that all the pseudo-dilutes described above were cinnamons, but the significance of this is doubtful.

TESTS FOR LINKAGE OF NAKED

In June, 1928, there were received at the BUSSEY INSTITUTION from Doctor N. G. LEBEDINSKY of Riga, Latvia, six albino mice, two males and four females, heterozygous for the dominant Mendelian character, naked. They were sent at the request of Doctor CASTLE, and brought to

this country through the kindness of Doctor HANS NACHTSHEIM of Berlin and Doctor SCHRATA. From these six parents were derived the stock used in the linkage experiments here described. The original albino naked animals proved to be vigorous and good breeders, and the F_1 generation from crosses with other mice was exceptional in these respects. F_1 naked females not uncommonly produced and raised litters of six to eight young, and one such female gave birth to thirteen young of which twelve were raised to two weeks of age.

To date linkage tests of naked with rodless, hairless, piebald, black-eyed white, agouti, brown, pink-eye, albinism, waltzing, dilution, and short-ear have been completed, in every instance with negative results. It can therefore be concluded that the gene for naked does not lie on any one of the eight chromosomes occupied by these characters. All data were derived from backcrosses, the fact that naked is dominant making it unnecessary to raise an F_2 generation. With a few exceptions, pregnant females were removed to isolation pens, thus avoiding any mistake as to the identity of the mother and providing more favorable conditions for the young. All litters were classified at two weeks of age or within a few days thereafter, as by three weeks loss of hair was usually so complete as to make identification of coat color difficult or impossible. In many cases a preliminary record of coat color was made prior to two weeks of age. The linkage data are summarized in table 5.

In the case of every character but one, short-ear, free reassortment with naked is unquestionable, most of the characters showing more than 50 percent of crossovers. Short-ear shows only 43.3 percent and a Dev./P.E. of 3.5; but in view of the fact that dilution shows 49.5 percent crossing over and a Dev./P.E. of only 0.1, it seems highly probable that the gene for naked lies in a different chromosome from that occupied by the genes for these two characters.

The figures showing absence of linkage with hairless also prove the two characters to be not allelomorphic. Mice which are both hairless and naked ($hrhrN_n$) can be identified by the short, rough coat prior to shedding, by the loss of hair on the feet at the fourteenth day, and especially by the wrinkled skin at from two to three weeks of age, though as they get older they become almost indistinguishable in general appearance from ordinary hairless mice.

THE LINKAGE OF HAIRLESS AND PIEBALD

The hairless mice used in the experiments here described were descended from one homozygous hairless male and two heterozygous hairless fe-

TABLE 5

Backcross data showing absence of linkage of naked with other characters.

CHARACTER	NON-CROSSOVERS		CROSSOVERS		*Expected Crossovers*	CROSSOVER PERCENT	DEV. / P.E.
Rodless	*Rn*	*rN*	*RN*	*rn*			
	7	8	12	12	*19.5*	61.5	2.1
Waltzing	*VN*	*vn*	*Vn*	*vN*			
	5	7	6	12	*15.0*	60.0	1.6
Hairless	*H^{r}N*	*h^{r}n*	*H^{r}n*	*h^{r}N*			
	13	14	19	22	*34.0*	60.3	2.5
Piebald	*SN*	*sn*	*Sn*	*sN*			
	28	32	42	33	*67.5*	57.0	2.4
Agouti	*AN*	*an*	*An*	*aN*			
	66	91	88	99	*172.0*	54.3	2.4
Brown	*BN*	*bn*	*Bn*	*bN*			
	67	79	88	80	*157.0*	53.5	1.8
Pink-eye	*PN*	*pn*	*Pn*	*pN*			
	45	45	50	54	*97.0*	53.6	1.5
Albinism	*Cn*	*cN*	*CN*	*cn*			
	15	15	14	10	*27.0*	44.4	1.2
Black-eyed white	*Wn*	*wN*	*WN*	*wn*			
	13	14	10	14	*25.5*	47.0	0.6
Dilution	*DN*	*dn*	*Dn*	*dN*			
	32	27	31	27	*58.5*	49.5	0.1
Short-ear	*S^{s}N*	*s^{s}n*	*S^{s}n*	*s^{s}N*			
	65	57	52	45	*109.5*	44.3	3.5

TABLE 6

Backcross data showing 1:1 ratio of naked to normal coat.

OBSERVED		*Expected*		DEV.	P.E.	DEV. / P.E.
Naked	Normal	Naked	Normal			
361	373	*367*	*367*	6	9.14	0.7

males derived from BROOKE'S original stock (BROOKE 1926). This stock has been maintained in CREW'S laboratory in Edinburgh. They were brought to this country by Doctor DUNN and very kindly given by him to the author.

Before any large amount of data had been gathered in crosses involving hairless and the various other coat characters in mice it became evident that hairless and piebald were linked. Thereupon all other linkage tests were dropped and every effort concentrated on this one experiment. By a fortunate coincidence the original hairless individuals were piebalds so that it was unnecessary to raise an F_2 generation to obtain double recessive individuals for a backcross. Moreover, the piebald which they carried was of a rather high grade and therefore excellent to work with as the homozygous and heterozygous piebald segregates were usually distinguishable from one another without the slightest difficulty.

Owing to the sterility of the hairless females it was impossible to use the usual backcross mating to test the crossover rate in doubly heterozygous males. Hence the following matings were used:

$$♀ \frac{Sh^r}{sh^r} \times ♂ \frac{sh^r}{sh^r}$$

$$♀ \frac{sH^r}{sh^r} \times ♂ \frac{SH^r}{sh^r}$$

The first of these is the ordinary backcross. The second was adopted in preference to an F_2 coupling cross because, while no more efficient in showing the presence of a linkage, it reveals crossovers in the male only. The crossover percent for this mating was calculated by a modification of the method of maximum likelihood described by R. A. FISHER (1928, pp. 243-244).

In order to insure the accuracy of the data gathered, the following precautions were adopted. All pregnant females (with a few exceptions due to failure to detect pregnancies) were isolated in separate pens. In some cases where the litter was large and the mother unable to furnish sufficient milk, all young in excess of three or four and occasionally the entire litter, were given, when between one and four days of age, to foster mothers. All litters were classified at two weeks of age or a few days thereafter, and in most cases preliminary records were made as to the self or piebald character of the coat at between ten and fourteen days of age.

Despite these precautions, the data are still subject to one possible

source of error. Though the piebald used was in general of a high grade it showed considerable variation, and it is thus possible that some individuals genetically homozygous piebald were phenotypically self, while others genetically heterozygous self were phenotypically piebald. Such

TABLE 7

Backcross data showing 1:1 ratio of haired to hairless.

OBSERVED		*Expected*		DEV.	P.E.	$\frac{\text{DEV.}}{\text{P.E.}}$
Haired	Hairless	Haired	Hairless			
92	101	*96.5*	*96.5*	4.5	4.69	1.0

TABLE 8

F_2 data showing 3:1 ratio of haired to hairless.

OBSERVED		*Expected*		DEV.	P.E.	$\frac{\text{DEV.}}{\text{P.E.}}$
Haired	Hairless	Haired	Hairless			
115	40	*116.25*	*38.75*	1.25	3.64	0.3

TABLE 9

Data showing the linkage of hairless and piebald.

MATING	*SH*^{r}	*Sh*^{r}	*sH*^{r}	*sh*^{r}	CROSSOVER PERCENT
$\frac{SH^r}{sh^r} \times \sigma^{\prime} \frac{sh^r}{sh^r}$	50	6	3	56	7.8 in ♀
$\frac{Sh^r}{sH^r} \times \sigma^{\prime} \frac{sh^r}{sh^r}$	0	2	7	1	10.0 in ♀
$\frac{NSH^r}{nsh^r} \times \sigma^{\prime} \frac{nsh^r}{nsh^r}$	27	4	5	32	13.3 in ♀
					Total 9.8 in ♀
$\frac{sH^r}{sh^r} \times \sigma^{\prime} \frac{SH^r}{sh^r}$	77	1	38	39	2.6 in ♂

individuals would have been classified as crossovers. In view of this difficulty, it would be desirable, were further linkage studies made, to test all supposed crossovers genetically. In the experiments here reported, only one individual, a female given me by Miss THIGPEN and thus not a product of my own crosses, was established genetically as a crossover.

She was of the constitution *Shr/shr*. Of the other crossovers about half are open to very little doubt owing to the clean-cut phenotype, but in view of the doubt as to the remaining half it is possible that the calculated crossover percent is somewhat too high.

The results are recorded in table 9. Those from crosses in which naked was involved are given under a separate heading, as they are slightly less reliable than the remainder owing to the difficulties of classification when naked is present. When totaled they show a crossover percent of 9.8 in the females and 2.6 in the males. It is of interest to note that in this linkage, as in that of pink-eye with albinism, the data show a higher crossover rate in the female than in the male.

PROBABLE MUTATIONS TO BLACK-AND-TAN

During the progress of the crosses here reported there occurred four probable mutations to black-and-tan. The mutants are listed in table 10, together with the date of their birth, and the known facts as to their own and their parents' genetic constitution. Unfortunately, at the time the mutations occurred, there were other black-and-tan individuals in the laboratory, so the evidence for the occurrence of mutation is not as convincing as in the earlier instance reported from the same laboratory by PINCUS (1929). In the case of female H382, however, a good check was possible. Her father, male H26, was the son of an albino and hence carried albinism. Her mother, female H66, on the other hand, was homozygous for color, as shown by the production of 16 young, all colored, when mated to male H26. All black-and-tan mice in the author's stocks, and so far as can be determined in the whole laboratory, were from lines probably not carrying albinism. Hence when female H382 was shown by mating to an albino male to carry albinism, she was fairly definitely established as the offspring of female H66 and male H26, both dark-bellied individuals, and therefore as a mutation.

Of the other possible mutants, H433 and H588 died before any breeding tests were possible, and S263 lacked characters which would have served as a possible check. H433 and S263 were born in pens from which females were not being isolated, so in each case the mother may have been either one of two females in the pen, both of which had litters at about the same time. H433 was noted at about 2 weeks of age as appearing perhaps slightly older than its sibs, a fact possibly indicating that it had been accidentally transferred from another cage. At the time, however, there were no black-and-tan individuals in neighboring pens. We

therefore regard these three cases as being, rather more probably than not, mutations to black-and-tan.

In only one of the above four cases, that of male S263, were both parents homozygous for non-agouti so only in this case can we be sure that the mutation occurred in a non-agouti rather than an agouti locus. In all the other cases, however, both the parents at least carried non-agouti (table 10).

These four probable mutations to black-and-tan, together with the one reported by PINCUS (1929), and four to white-bellied agouti reported by LITTLE (1916), indicate that the light-bellied form appears much more

TABLE 10

Probable mutations to black-and-tan.

MUTANT	DATE OF BIRTH	MOTHER	FATHER
♂ S263 *a^{t}addPPD^{w}D^w*	March 28, 1929	♀ S100 *aaBBDdPpD^{w}D^w* or ♀ S101 *aaBbDdPpD^{w}d^w*	♂ S103 *aaDdPpD^{w}d^w*
♀ H382 *a^{t}aBbCcH^{r}h^{r}RR?Ss*	April 20, 1929	♀ H66 *aaBbCCH^{r}h^{r}ssS^{e}s^e*	♂ H26 *AaBbCcH^{r}h^{r}RrSs*
H433 *a^{t}add*	April 27, 1929	♀ H57 *AabbDdH^{r}h^{r}ss* or ♀ H17 *aaBbH^{r}h^{r}ss*	♂ H119 *AaBbCcDdH^{r}h^{r}RrSs*
H588 *a^{t}a*	June 11, 1929	♀ H271 *AaBbH^{r}h^{r}ss*	♂ H429 *AabbH^{r}h^{r}SsS^{e}s^e*

frequently as a mutation than the other known dominant characters of the house mouse. Comparison as to mutation rate with the known recessive characters is at present impossible owing to the much greater difficulty of detecting recessive mutations.

SUPPLEMENTARY EFFECTS OF THE GENE CAUSING SHORT-EAR

The gene for short-ear manifests itself principally by a reduction in the length of the ears, but other effects are also produced. Thus, GATES (1926a) has remarked that it produces morphological variations of the head and skull, and there is evidence that it causes reduction in general size and viability. Kinky-tail is also an effect of this gene as my data show, and not the effect of a linked gene.

In table 11 are recorded the mean measurements of the skulls of thirteen short-eared ($s^e\ s^e$) and twelve normal-eared ($S^e\ s^e$) mice, each measurement being expressed as a percentage of the basilar length, and accompanied by its probable error. In the next to the last column is found the difference of the means and the probable error of the difference. In the last column is given a measure of the significance of the difference, P, the values of P being calculated from formulae and tables given by R. A. FISHER (1928, p. 107 and p. 139). Values of P of 0.05 or less may be taken to indicate a surely significant difference. This test of significance is more accurate for small samples than the test furnished by Dev. / P. E.

TABLE 11

Mean measurements of the skulls of 13 short-eared ($s^e s^e$) and 12 normal-eared ($S^e s^e$) mice. Each measurement is expressed as a percentage of the basilar length (A).

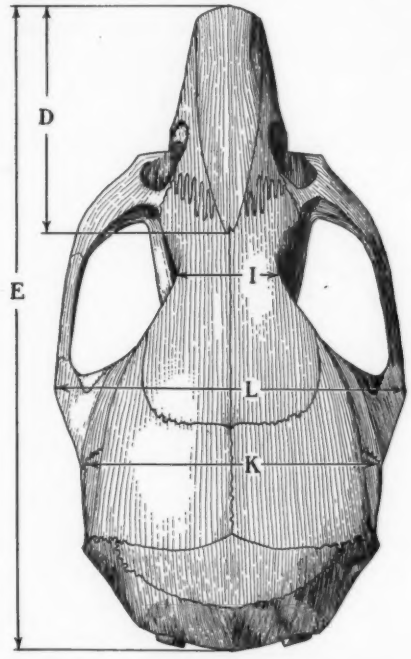
	MEASUREMENT	NORMAL-EARED	SHORT-EARED	DIFFERENCE	P
B	Condylo-basal length	120.27±.16	120.05±.17	.22±.24	.47
C	Length of tooth row	20.27±.11	20.13±.10	.14±.15	.46
D	Length of nasal bone	44.37±.28	43.95±.31	.42±.42	.45
E	Distema	31.07±.20	30.68±.10	.39±.22	.15
F	Greatest length	125.78±.32	124.58±.30	1.20±.30	.05
G	Palatilar length	55.68±.12	54.92±.13	.76±.17	P<.01
H	Width across auditory bullae	42.71±.27	42.38±.34	.33±.44	.57
I	Interorbital width	21.09±.17	21.35±.16	.26±.23	.40
J	Width foramen magnum	24.22±.11	24.62±.21	.40±.23	.21
K	Width brain case	56.14±.27	57.38±.29	1.24±.40	.03
L	Zygomatic width	64.47±.26	65.60±.25	1.13±.37	.03
M	Width outside molars	26.33±.11	26.85±.12	.52±.16	.02
N	Maximum height	37.36±.18	37.75±.32	.39±.36	.43
O	Height from basion to inion	34.17±.16	34.74±.17	.57±.24	.08
P	Height of rostrum	19.83±.10	17.42±.15	2.41±.18	P<.01

All twenty-five skulls used were obtained from eight litters from matings of the type ♀ $S^e\ d/s^e\ D \times$ ♂ $s^e\ d/s^e\ d$ so that the short-eared individuals were sibs of the normal-eared controls. Hence it may be safely concluded that all differences noted are due to the action of the gene for short-ear and not to any multiple factor differences present in the short-eared and normal-eared strains.

All measurements were made with vernier callipers.

Of the measurements used (figures 5, 6, 7, and table 11), A, B, C, E, G, J, K, L and N were employed by GATES (1926a); D, F, I, and M were suggested by Doctor ALLEN; O was adopted from JAYNE (1898, p. 509); and H and F were developed to show special peculiarities of the short-eared skull. They reveal that the skull of short-eared mice is proportion-

ately shorter and wider than that of normal-eared, the palatiler length being especially reduced. Even more marked is the reduction in the height of the rostrum. These changes account for the slightly stubby-nosed appearance of the short-eared mice. Of the measurements of width, only one, that across the auditory bullae, was less for the short-eared than the normal-eared, this slight reduction of the bones in the region of the ear being a natural accompaniment of the reduction of the external ear itself.



FIGURES 5, 6, and 7.—Three views of mouse skull, showing the measurements used. In figure 7, the right auditory bulla is removed.

In addition to the cranial measurements, some preliminary measurements similar to those used by GATES (1926a) were made on various features of the external anatomy, but as these failed to reveal any new differences between the two genetic types they were discontinued. Weighings of the two types indicated that the short-eared mice probably average smaller than their normal sibs, but a larger number of weighings than

has so far been made will be necessary to establish the difference statistically. The difference in viability has already been mentioned.

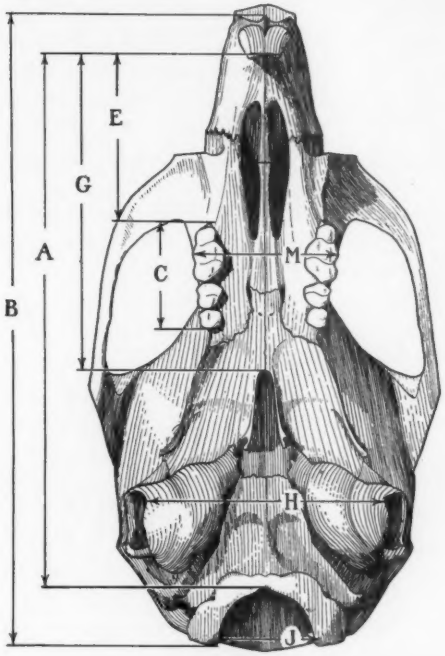


FIGURE 6.

FIGURE 7.

SUMMARY

A description is given of most of the unit characters that have been reported in the house mouse.

The recessive and dominant forms of hairlessness are proved to be due to different genes located on different chromosomes. Recessive hairless is established as a clear-cut Mendelian character.

Data are presented showing the absence of linkage of dominant hairless or naked with rodless, hairless, piebald, black-eyed white, agouti, brown, pink-eyed, albinism, dilution, short-ear, and waltzing.

A close linkage of hairless with piebald is established. Three hundred forty-eight young from matings made to measure the intensity of the linkage show a crossover percent of 9.8 in the female and 2.6 in the male.

New data on the linkage of short-ear and dilution are reported. In a backcross generation of 1140 young, of which 106 were raised by Miss COPELAND at SMITH COLLEGE, 1 crossover was obtained by Miss COPELAND, none by the author.

Measurements are given of the skulls of 13 short-eared and 12 normal-eared mice which show the gene for short-ear to produce pronounced changes in the shape of the skull, especially a proportionate increase in width of the brain case and a reduction in height of the rostrum. Kinky-tail is also shown to be due to this gene and not to a closely linked gene as has been twice reported.

Three cases of reversal of dominance in young mice of the gene for dilution are described. These mice, all heterozygous for dilution, appeared dilute when young but changed to intense when they grew older.

Mention is made of 4 probable mutations to black-and-tan.

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STERILITY IN WILD ROSES AND IN SOME SPECIES HYBRIDS

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Most botanists agree that there occur in nature many spontaneous hybrids between related rose species (BOULENGER 1929), and it has been found that wild individuals often exhibit a considerable amount of aborted pollen. HUSKINS (1929) pointed out that neither meiotic irregularities nor pollen sterility can be used as a certain criterion for hybridity, because the balanced conditions necessary for regularity during meiosis may be upset by other agencies besides hybridization. Nevertheless it cannot be denied that these phenomena are as JEFFERY (1929) states "outstanding features of the reduction division of hybrids."

HURST (1925, 1928) bases the experimental testing of his theory of differential polyploidy in Rosa upon the contention that any two diploid species from one of his five fundamental species groups will give "fully fertile" offspring, while any two from two different fundamental species will give sterile hybrids. It was therefore of interest to discover the actual state of fertility and its variation among our wild roses, as well as to make some crosses using parents with known pollen sterility.

The percentage of shrivelled grains in pollen from thirty-seven individuals, collected in 1927, has been given by the writer (ERLANSON 1929). These samples were stored over calcium chloride and examined dry. Since

[1] Paper from the Department of Botany of the UNIVERSITY OF MICHIGAN, No. 326, representing work carried on under a National Research Fellowship in the Biological Sciences.

then pollen from three hundred and sixty individuals collected in 1928 and 1929 has been examined. It was first measured dry and then treated with aceto-carmine, which causes the grains with contents to swell and stain, and greatly facilitates counting. Pollen from the same individual has been examined for empty grains both dry and after treatment, and similar results were obtained by both methods. It was found necessary to count about 400 grains in each sample in order to get a reliable result, since, when the amount of sterile pollen is high, there is apt to be a clumping of the shrivelled grains in some parts of the field under a 3 mm. lens. The plants from which pollen samples were taken are all growing in the Botanical Garden of the UNIVERSITY of MICHIGAN.

VARIATION IN STERILITY WITHIN THE SPECIES

The pollen sterility in eight groups of North American wild roses, mean sterility and variation among a given number of individuals selected at random are shown in table 1. The percentage of pollen grains without contents is given.

TABLE 1

Mean pollen sterility in wild rose species groups.

GROUP	CYTOLOGICAL CLASS	NUMBER OF INDIVIDUALS	PERCENT MEAN STERILITY	PERCENT VARIATION IN STERILITY
R. blanda	Diploid	28	20.9	2.0 – 57.3
R. Woodsii	Diploid	28	23.7	4.0 – 62.7
R. palustris	Diploid	12	8.0	0.2 – 21.75
Species indet.	Triploid	4	94.0	86.0 – 100.00
R. virginiana; R. carolina	Tetraploid	28	19.3	7.0 – 51.6
R. arkansana; R. suffulta	Tetraploid	28	26.1	8.0 – 49.0
R. californica	Tetraploid	4	23.3	19.3 – 26.0
R. acicularis	Hexaploid	23	7.5	0.0 – 17.5

In partially sterile pollen many of the grains though apparently perfect morphologically are not able to function in fertilization, as has been found in grapes (DORSEY 1914), in wheat (SAX 1922, WATKINS 1924) and in Nicotiana (EAST 1921). It is therefore probable that the total pollen sterility is actually higher than shown by my figures, since no tests of pollen germination were made. More samples of pollen have been examined from *R. blanda* Ait. than from any other species but only the first twenty-eight have been included in table 1, in order to make the comparison between this and the other species groups more equal. In figure 1 the variation in pollen sterility in five groups of roses has been plotted in classes differing by 10 percent of empty grains, and a larger number of

individuals are included in the graph for *R. blanda*. These graphs and table 1 bring out strikingly the small amount of empty pollen present in the hexaploid group of *R. acicularis* Lindl. and the diploid *R. palustris* Marsh. as compared with the other species. Although only a few counts have been made for *R. palustris*, it is the least variable of the eastern diploid species and these records probably give a true picture of its pollen

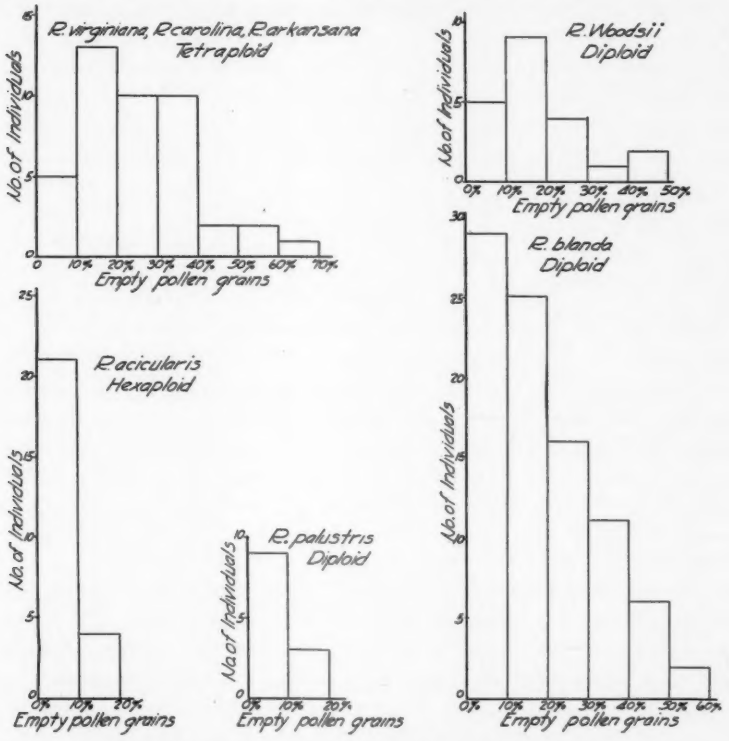

FIGURE 1.—Variation in pollen sterility in five groups of wild roses.

conditions. The two large and widespread diploid groups of *R. blanda* and *R. Woodsii* Lindl., and all the tetraploid roses examined, show an average of one-fifth to one quarter of empty pollen grains. The range in variation among individuals from each group is large, some having almost perfect pollen morphologically. Variation in pollen sterility is found in all cultures of any size and throughout the range of the various species. In the

European species *R. pimpinellifolia* L., *R. cinnamomea* L., and *R. arvensis* Huds., all of which have balanced chromosome complements, SCHWERTSCHLAGER (1910) found that the percentage of shrivelled pollen grains reached 20 to 25 percent in some individuals.

HARRISON and BLACKBURN (1927) gave the percentage of good pollen found in the various species groups of the section Caninae. They do not record the number of plants examined and, since the greatest range in variation given for any species is only 20 percent, it is probable that only a few samples were analysed for each. My figures bring out very strikingly the fact that in all the diploid and tetraploid groups on this continent (with the exception of *R. palustris*) there seems to be a segregation in the factors causing sterility, giving some plants with almost perfect pollen, morphologically, and others with as much as 50 percent aborted grains. In the group of *R. californica* C. et S. only four plants have been examined because these roses are scarcely hardy at Ann Arbor. NICOLAS (1927) has found that different plants of the same species show a great difference in fertility (fruit production) and attributed it to soil and habitat variation. That it may be due to inherent variation in sterility is shown by the fluctuations found in cultures grown under uniform conditions at Ann Arbor.

The Caninae all exhibit unpaired chromosomes at diakinesis and there is a large proportion of empty grains in the pollen of most of them (HARRISON and BLACKBURN 1927). In the cultivated Rubi LONGLEY (1927) finds indications of an association existing between even chromosome numbers and the production of fertile pollen. Table 1 shows that the few wild triploid rose individuals discovered thus far have amost completely abortive pollen. In the classic hybrid *Primula floribunda* × *P. verticillata* the sterile diploid F_1 plants have normal and regular maturation divisions, the contents of the microspores later disintegrating (DIGBY 1912, NEWTON and PELLEW 1929). A similar condition was reported in cultivated grapes by DORSEY (1914). An example of this type of pollen sterility associated with regular meiosis was described by the writer in a tetraploid Oregon rose related to *R. Durandii* Crépin which had 54.6 percent of the spores empty (ERLANSON 1930). I have come across two other tetraploid individuals and one diploid in which all the chromosomes usually pair at diakinesis, and which have over 2/3 of the mature pollen grains empty. The pollen of the tetraploid plants has been examined for more than one season, and some yearly fluctuation in sterility is shown, but the amount of empty grains is always of the same order. These amounts are listed as percentages in table 2.

R. relicta Erlanson is a dwarf from Illinois related to the tetraploid *R. arkansana* Porter. It sets very little fruit and shows some irregularities during meiosis (ERLANSON 1929). The plant N117, found in a diploid culture from *R. blanda* var. *glandulosa* Schuette, shows fourteen pairs at diakinesis, produces few flowers and has not set any fruit. It will be discussed in a future paper. A plant of the irregular tetraploid species *R. mollis* Sm. (Section Caninae) had only 67 percent of empty grains in 1929. The highly sterile specimen of *R. Fendleri* Crépin was sent from the Medicine Bow Mountains, Wyoming. It is not very vigorous but usually bears some fruit.

TABLE 2

Percentage of empty grains in pollen of three plants with all chromosomes pairing and with high sterility.

SPECIES AND ACCESSION NO.	1927	1928	1929
R. relicta (8320)	56 and 77	88	63
Species indet. (N117)		70.8	65
R. Fendleri (3720/A)			78

TABLE 3

Variation in pollen sterility among the offspring of individual wild roses.

SPECIES, ACCESSION NO., AND WILD ORIGIN	YEAR	PERCENTAGE OF EMPTY GRAINS (CLASS CENTERS) 2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
DIPLOIDS													
R. blanda, 3753/5, Michigan	1928	3	7	3	1	1	3	1					
R. blanda, 3753/6, Michigan	1929		1	3	3	1	1	1		1	1	1	1
R. blanda var. 3753/9	1928		3	1		2		2	1				
R. blanda var. *hispida*, 5773, Manitoba	1929		1	1			2						
R. blanda var. *hispida*, 9655, Manitoba	1929		1								1		
R. Woodsii, 4477, South Dakota	1929	1	1	4	2	1							
R. palustris, 5590, New Jersey	1929	1	2	2		1							
TETRAPLOIDS													
R. carolina, 3532, Michigan	1929			2		3		2				1	
R. suffulta, 2897b, Iowa	1929			2	1			1		1			

The variation in the amount of empty pollen grains in different individuals in cultures from wild diploids and wild tetraploids is shown in table 3. In each case the plants in a culture were the offspring of one wild seed parent. Column two gives the year in which the pollen was collected. These figures indicate a high degree of heterozygosis.

Table 4 contains the percentages of empty grains found in some wild diploid species of which there are only a few individuals at the Michigan Botanical Garden. In view of the fact that external conditions have been found to cause pollen sterility, it is interesting to observe the small amount of empty pollen in the specimens of *R. pisocarpa* A. Gray, since these are barely hardy in Michigan, being frozen back to the ground every two or three winters.

Rosa microphylla Roxb. is tender at Ann Arbor and rarely flowers. A plant which flowered in 1929 showed 29.3 percent of empty pollen grains. This plant is one of a very uniform culture and the species is not closely related to any other rose. In the pollen studies of CLEMENTS and PENLAND (1925-1926) they found that very few species in nature produce

TABLE 4

Percentage of empty grains in pollen of miscellaneous diploids in 1929.

SPECIES, ACCESSION NUMBER, AND WILD ORIGIN	STERILE POLLEN
R. rugosa, 5311, Tennessee (escaped)	22.8
R. foliolosa, 9526, Texas	52.5 (July 17); 50 (August 2)
R. foliolosa, 9529, Arkansas	11
R. ultramontata, 9658, British Columbia	5
R. pisocarpa, 4632	8.5
R. pisocarpa, 4634, Oregon	12.3

over 95 percent of good pollen, and they suggested three classes according to the percentage of sterile pollen, namely, with 50 percent and over of sterile pollen, with 20 to 50 percent, and under 20 percent. My pollen examinations show that the proportion of empty pollen grains in any group or species of Rosa may vary from about 5 percent to 25 percent. This amount of sterility may not be of much significance in relation to the detection of natural hybrids, but rather due to physiological and ecological conditions. This matter will be referred to again in connection with sterility in known hybrid roses.

DIPLOID AND TETRAPLOID *R. SUBSERRULATA*

A diploid plant of *R. subserrulata* Rydberg (No. 9528), discovered in 1927 (ERLANSON 1929) had 24.8 percent empty microspores in 1929. This plant was sent from Oklahoma by Mr. RALPH SHREVE. It has always been very weakly in vegetative growth and all parts, including the flowers, are smaller than in the normal tetraploid race. It has been severely attacked by anthracnose the past two seasons. It may have originated as a

haploid from a normal tetraploid, or it may have been produced from a triploid hybrid by the union of two gametes possessing only seven chromosomes. Another plant of *R. subserrulata* (No. 7697) sent by Mr. SHREVE from Arkansas, is a normal vigorous tetraploid plant. It had 7.8 percent of empty pollen grains in 1929. The abnormal chromosome number of the diploid *R. subserrulata* is not revealed by any unusual amount of sterile pollen, but rather by the depauparate habit.

STERILITY IN INTERSPECIFIC HYBRIDS

Beginning in 1925 many crossings have been made between species growing in the rose collection at Ann Arbor. The difficulty with which rose seeds germinate is well known. If the seeds germinate promptly the seedlings of most species reach maturity in their third season. It is not surprising, therefore, that there were not many F_1 plants mature in 1929. Table 5 shows the variation in the amount of aborted pollen in the members of some F_1 cultures, two of which had diploid parents and four tetraploid. In each instance the parents belonged to closely related species.

I. R. Schuettiana Erlanson × *R. acicularioides* Schuette

Both these species are possibly descended from *R. blanda* by natural hybridization, with *R. palustris* to give *R. Schuettiana* and with *R. aciculars* to give *R. acicularioides*. The particular plants used in this cross both show under 14 percent of empty pollen grains. In nine F_1 plants only one had more than 14 percent and the mean sterility for the hybrid plants was less than the mean sterility for the two parents. The parent species are seemingly completely compatible. The results from this cross suggest that the production of an amount of pollen up to about 20 percent may be an innate characteristic in plants which may be considered as "fertile" wild rose individuals. The F_1 hybrids are fairly uniform in appearance and resemble *R. blanda*. They are extremely floriferous and the inflorescence tends to be compound. The stems, new shoots and foliage are richer in anthocyanin pigmentation than in typical *R. blanda*. A good crop of hips and achenes is obtained by open field pollination, but very few seeds are produced after artificial self-pollination. I have often found indications of self-sterility in *R. blanda* and in other wild roses, another factor adding to the difficulties of genetical work in this genus.

Garden plants of *R. Schuettiana* have been grown from the type clump only, but we have several plants of *R. acicularioides* from different stations which show great diversity in pollen sterility, one plant having 43 percent of empty grains. Therefore it cannot be concluded that the cross

TABLE 5

Pollen sterility of F_1 hybrids compared with that of parents.

DIPLOIDS

I. *R. Schuettiana*×*R. acicularioides.* Accession No. 11812.
Sterile pollen: Seed parent, (1928) 2 percent, (1929) 12 percent. Mean 7 percent
Pollen parent, (1929) 13.75 percent.
9 F_1 plants. Variation in percentage of sterility 1929.

2.5	7.5	12.5	17.5
1	6	1	1

Mean sterility of F_1, 7.7 percent.
Mean sterility of parents, 10.4 percent.

II. *R. subblanda*×*R. blanda var. Hermanni.* Accession No. 11810
Sterile pollen: Seed Parent, (1929) 2 percent.
Pollen Parent, (1927) 6 percent, (1928) 6 percent.
19 F_1 plants. Variation in percentage sterility. 1929.

2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5
1	5	1	5	1	2		2		2

Mean sterility of F_1, 21.7 percent.
Mean sterility of parents, 4 percent.

TETRAPLOIDS

I. *R. virginiana*×*R. carolina.* Accession No. 11809.
Sterile pollen: Seed parent, (1929) 21.2 percent.
Pollen parent, (1929) 21.4 percent.
2 F_1 plants, pollen sterility, 12.25 percent and 14.5 percent. Mean, 13.4 percent.

II. *R. Lyoni*×*R. carolina.* Accession No. 11815.
Sterile pollen, Seed parent, (1929) 16 percent.
5 F_1 plants, pollen sterility, 10.5, 19, 21, 22.7, and 25.5 percent. Mean 19.7 percent.

III. *R. virginiana*×*R. obovata.* Accession No. 11811.
Sterile pollen, Seed parent, (1929) 21.2 percent.
2 F_1 plants, pollen sterility, 9.75 percent, 12 percent. Mean, 10.9 percent.

IV. *R. suffulta*×*R. carolina* (*R. rudiuscula* Greene) Accession No. 11817.
Sterile pollen in parents unknown.
1 F_1 plant, sterile pollen, 25.5 percent.

R. Schuettiana × *R. acicularioides* would give fertile hybrids invariably. When HURST (1925, 1928, 1929) proposed breeding as a test for relationship in wild species, he cannot have been aware of the great differences in fertility among plants which belong morphologically to the same species.

II. R. subblanda Rydberg × *R. blanda* var. *Hermanni* Erlanson

The plants used in this cross both belong within the collective species *R. blanda, R. subblanda* differing from the type of *R. blanda* chiefly in its glabrous foliage. Both parents had exceptionally "good" pollen, yet among nineteen F_1 individuals the amount of empty pollen grains varied from 2 percent to 46 percent in 1929. The mean sterility of the hybrids was 17.7 percent greater than the mean sterility of the parents. If the results were used to test whether the parents belong to the same "fundamental diploid species" of HURST, or not, it would be difficult to decide. Certainly the hybrids are not completely sterile, but if one by chance had only those with over a third of the pollen abortive the classification would be still more puzzling, since HURST does not allow for the possibility of "semi-sterile" diploid hybrids. The *R. subblanda* parent happened to have very little aborted pollen, but this condition is not characteristic for all individuals of the species. Another plant, from Missouri, had 57 percent of the microspores lacking contents, also in 1929.

The achenes of one of these F_1 plants which had 7.5 percent empty pollen grains, were examined. In four hips a total of 83 large achenes and 34 aborted ovaries were found. Only 71 of the achenes contained embryos.

The F_1 plants in this culture show segregation in colour of stigmas, filaments and petals, and with regard to pubescent and glabrous foliage. Therefore it is evident that in spite of the high pollen fertility of the parents they were not homozygous for these characters.

The conclusion to be drawn is that the processes of mutation, crossing over and so forth, have proceeded in different directions in these two related forms, rendering them partially incompatible when interbred. BOULENGER (1929) found a series of plants which he suspected of being hybrids between the two diploid species *R. arvensis* and *R. sempervirens*. He sent pollen samples from the same sets of plants to two men who obtained widely different results as to the percentage of bad pollen. However, by both investigators the suspected hybrids were found to have more sterile pollen than either of the parents. Both these species are placed by HURST in his fundamental species AA, and should give "fully fertile" hybrids.

III. Tetraploid hybrids

The plants used in the first three crosses listed under tetraploids in table 5 are all suspected of hybridizing in nature. BEST (1887) at one time proposed to make *R. virginiana* Mill and *R. carolina* L. and the related forms all varieties of one species, but this suggestion has not been generally

followed because of the distinct habit of *R. virginiana* as compared with the others.

Two F_1 plants from *R. virginiana* × *R. carolina* had a mean pollen sterility 8 percent less than that of the two parents.

The tetraploid forms *R. Lyoni* and *R. carolina* are closely related, *R. Lyoni* being a strongly pubescent and vigorous form. The five F_1 plants obtained from crossing these roses all show fairly good pollen, the mean sterility of the hybrids being only 3.7 percent greater than the sterility of the seed parent. The sterility of the pollen parent was not ascertained.

Two tetraploid hybrids obtained from *R. virginiana* × *R. obovata* show unusually low amounts of abortive pollen grains, only half as much as that shown by the seed parent. The sterility of the pollen parent in this cross is also unknown. *R. obovata* Raf. is very doubtfully distinct from *R. carolina* L.; it was described as *R. humilis grandiflora* by Baker (*R. humilis* Marsh = *R. carolina* L. 1753 not 1762).

The tetraploid hybrids I and III in table 5 produce abundant pollen and a good crop of fruit. This is an indication that *R. virginiana* is closely related to *R. carolina* and its varieties and it may be said, in these instances, to be completely compatible with them in hybridization, judging from the fact that none of the hybrid plants has over 20 percent of empty pollen grains, nor a higher sterility than the parent plant of *R. virginiana* used in the experiments. In HURST'S cytological classification (1928, 1929) he classes *R. humilis grandiflora* Baker (*R. obovata* Raf.) as AADD and *R. virginiana* as CCDD. Each capital letter designates a set of seven homologous chromosomes. Following this scheme the hybrids from *R. virginiana* × *R. obovata* would be ACDD, unbalanced tetraploid plants with seven pairs and fourteen univalent chromosomes at first meiotic metaphase. These plants have not been examined cytologically, but one would expect them to have a greater amount of poor pollen than the balanced tetraploid parents.

A plant of *R. suffulta* Greene was crossed with *R. carolina* in 1925 and one F_1 plant was raised, which flowered first in 1928. This plant is of particular interest because it resembles the form *R. rudiuscula* Greene, a highly variable species found in the central United States along the Mississippi Valley, in the region where the ranges of *R. carolina* and *R. suffulta* overlap. The hybrid plant has only a quarter of the pollen grains empty and a wild plant sent from Missouri by Mr. B. F. BUSH had 23.5 percent aborted pollen in 1929.

IV. Miscellaneous diploid species hybrids

The amounts of empty pollen grains in four miscellaneous species hybrids not made by myself, which are in the collection of the UNIVERSITY OF MICHIGAN, are shown in table 6, together with the classification of the parents involved according to HURST'S scheme.

HURST places *R. palustris* Marsh. among the tetraploid species. Our plants are diploid and are probably his diploid "*R. carolina*" which he designates as a DD species (HURST 1928, 1929). The plants involved in each of the hybrids listed in table 6 happen to belong to HURST'S fundamental diploid species CC and DD. The hybrids are therefore all CD, and should be "completely sterile." The hybrid *R. foliolosa* × *R. rugosa* alone fulfills this condition. It was found to be completely sterile in 1928. It was scarcely hardy in Michigan and has been sent to California for further observation. In 1928 a plant appeared, in an isolated bed among bushes of *R. blanda* and *R. subblanda*, which had distinctly rugose foliage. It is thought to have originated from a chance pollination of *R. blanda* by *R. rugosa* Thunb. This plant bears good fruit but shows more abortive pollen than either of the plants of *R. Tetonkaha* Hansen. It produces, however, a larger amount of pollen than the latter.

TABLE 6

Pollen sterility in miscellaneous diploid hybrids (Hort.).

PARENT SPECIES	F_1 ACCORDING TO HURST	PERCENT OF EMPTY POLLEN IN HYBRID PLANTS
R. rugosa×*blanda* (*R. Tetonkaha* Hansen)	*CC*×*DD*	16.4
		12.0
R. blanda×*rugosa* (spontaneous)	*DD*×*CC*	38.6
R. palustris×*rugosa* Hort. Amst.	*DD*×*CC*	6.0
		14.7
R. foliolosa×*rugosa* (S. P. I. 63685)	*DD*×*CC*	100.0

R. Tetonkaha was produced by HANSEN by crossing a hybrid *R. rugosa* with a native wild rose in South Dakota, probably *R. blanda*. Our plants closely resemble the illustration of *R. Warleyensis* Willmott, a plant which was judged by Miss WILLMOTT (1914) to be *R. blanda* × *rugosa*, except that extra petals are frequent in the flowers of *R. Tetonkaha*. The low percentage of sterile pollen in the two plants of *R. Tetonkaha* (table 6) is somewhat misleading, because these plants usually produce only a small amount of microspores in each anther. One of these individuals was examined cytologically and was found to have seven pairs at diakinesis and to ex-

hibit very little polyspory (ERLANSON 1929). The plants set good fruit. Under HURST'S scheme there should be no pairing of chromosomes at meiosis in these hybrids and they should be sterile. Judging by external morphology one would not place *R. blanda* and *R. rugosa* in the same collective species. The production of supernumerary petals and the deficiency of mature pollen would be indicative of the hybrid nature of these plants of *R. Tetonkaha* if their origin were unknown. The tetraploid F_1 hybrids listed in table 5 do not exhibit these characteristics.

Seed of the hybrid *R. palustris* × *rugosa* were obtained from the BOTANICAL GARDEN at Amsterdam, Holland, and our plants are perhaps F_2 hybrids. Several of the plants of this culture resemble strongly the *rugosa* parent. These have never bloomed. Two plants which have many characteristics in common with the *palustris* parent show very little sterile pollen and bear several hips containing plump achenes each year. They seem to exemplify segregation in F_2 of a partially sterile hybrid into sterile and more fertile types, as reported by KRISTOFFERSON (1926) to occur in interspecific *Malva* hybrids.

V. Hexaploid hybrid

A hexaploid F_1 plant of *R. Engelmanni* × *R. acicularis* var. *Sayiana* flowered for the first time in 1929 and had 6.6 percent of the pollen grains aborted. The female parent had 13.3 percent of empty grains in 1927 and the male parent 5.3 percent in 1929. *R. Engelmanni* S. Wats. is closely related to *R. acicularis* var. *sayiana* Erlanson, although HURST classifies the former as BBDDEE and the latter as CCDDEE.

VARIATION IN POLLEN STERILITY IN THE SAME INDIVIDUAL IN ONE SEASON

CRÉPIN (1889) reported that in his studies of pollen sterility in wild roses he found that the amount varied from bud to bud on the same bush as well as from year to year. My own observations show that the sterility in two samples from the same bush taken in one season usually varies very little. Some examples are listed in table 7. The large variation in sterility in *R. relicta* is anomalous, this type being one of the balanced tetraploids with high sterility referred to above. It is evident that the amount of lagging at reduction division in this plant differs from bud to bud. The average variation in percentage of sterility for the ten diploid individuals listed in table 7 is 4.3, which is very close to the average difference in sterility from one season to the next for twenty diploid individuals and for eight tetraploids listed in table 8.

TABLE 7

Variation in the percentage of empty grains in pollen samples taken from the same individual in the same season.

SPECIES AND SOMATIC NO.	RANGE OF STERILITY IN PERCENT
R. blanda (2x=14)	24.7–38.0
	30.0–41.6
	3.0– 5.0
	9.5–11.0
	4.0– 5.0
	11.0–16.0
	15.0–20.0
R. Woodsii (2x=14)	20.3–21.6
R. palustris (2x=14)	12.0–21.75
R. subserrulata (2x=14)	26.2–31.0
R. carolina (2x=28)	30.0–34.0
	20.2–22.7
R. relicta (2x=28)	56.0–77.0
R. acicularis (2x=42)	6.0– 7.5
	7.0– 7.8
R. muriculata (2x=42)	12.5–14.0

VARIATION IN POLLEN STERILITY IN THE SAME INDIVIDUAL FROM SEASON TO SEASON

Increase in pollen sterility has been induced in several genera by exposing the plants to abnormal temperatures. STOW (1926-1927) found that high temperatures would cause pollen sterility in *Solanum tuberosum*. An increase in pollen sterility was obtained at high temperatures by SAKAMURA and STOW (1926) in *Gagea lutea*, and by HEILBORN (1928) in cultivated apples. Cold caused an increase in the number of aborted pollen grains in *Datura* (BLAKESLEE and CARTLEDGE 1927). Sterility induced by gall mites in *Lycium halimifolium* was reported by KOSTOFF and KENDALL (1929).

Temperatures in Michigan are notoriously variable. The first flower buds of the early-flowering octoploid and hexaploid roses in the group of *R. acicularis* were killed by frosts late in May, 1929, and some buds in this group and also in *R. Woodsii* had their petals destroyed by the late cold spell. Early in June there is often a hot dry period, which may be followed by cold rains before the heat of July with its drying winds. Since temperature has been found to affect the amount of pollen sterility it was of interest to find out to what extent the latter fluctuated in different years in the same rose plant. Should the amount of sterile pollen vary greatly from one year to the next it would be obviously useless as a cri-

TABLE 8

Percentage of empty pollen grains in the same individual rose for two different seasons.

SPECIES AND ACCESSION NUMBER	PERCENT OF EMPTY POLLEN GRAINS			DIFFERENCE
	1927	1928	1929	
DIPLOIDS				
R. subblanda Rydberg 2681/D		8.5	8	0.5
R. blanda var *Hermanni*, 2686/B	6	6		0
R. blanda Ait.				
2895/A	10	12.2		2.2
5819/A		5	0.75	4.25
8332/A		5	6	1
3502/A	52	53.3		1.3
3753/5/N8		27.5	25	2.5
5/N9		31.6	33.3	1.7
5/N13		5	9.6	4.6
5/N15		9	14.5	5.5
R. blanda var. *hispida*, 5773/D		20	28	8
R. subblanda × *R. blanda*				
11810/N5		9	6.5	2.5
N14		10	16.4	6.4
N17		26.5	29	2.5
R. Schuettiana Erlanson, 5891/A	8.3	2	12	10
R. acicularioides Schuette, 6452/A		3 and 5	5	2
8261/A		45.6	43	2.6
R. Woodsii Lindl., 2882/A		29	28	1
R. Fendleri Crépin, 3720/D		62.7	50	12.7
R. subserrulata Rydb., 9528/A		27 and 31	24.8	6.2
			Mean	3.8
TETRAPLOIDS				
R. virginiana Mill., 4651/B	10		10.7	0.7
" 5780/A		8	7	1
R. rudiuscula Greene, 4293/B		32.3	23.5	8.8
R. arkansana Porter, 5771/G		16	24	8
" 6424/N1		80	79	1
R. suffulta Greene, 2682/D	15.5		17.6	2.1
" 2897b/C		49	45.2	3.8
" 3001/A	29	23.1		5.9
R. polyanthema Lunnell, 6368/A		15.2	46.9	31.7
R. relicta Erlanson, 8320/A	56 and 77	88	63	32
HEXAPLOIDS				
R. acicularis Lindl. var. *lacorum*, 6008/N6	8.4	7 and 7.8	6	2.4
R. Engelmanni S. Wats., 6080/A		5.8	2	3.8
R. muriculata Greene, 2931		7	12.5 and 14	7
TRIPLOIDS				
2949/A	92.7	86.7	86	6.7
5590/N2	97	94	93	4

terion for hybridity. The percentage of empty grains in pollen samples from thirty-six different individuals for two, and sometimes three, seasons is given in table 8. In the last column the difference between the highest and lowest percentage is given for each individual. Among the diploid plants considered there are nine in which there was a greater amount of aborted pollen in 1929 than in 1928 and eight in which there was less. All these plants come into flower about the same time, which indicates that cold at least has a negligible effect upon reduction division in the pollen mother cells of these roses. The mean variation in the percentage of aborted pollen for two seasons in twenty diploid individuals is only 3.8 percent.

Among the ten tetraploids listed in table 8, two show an abnormally large variation in the amount of aborted pollen in two consecutive seasons. These are *R. relicta* Erlanson, which was referred to in this respect above, and the other is a plant of *R. polyanthema* Lunnell from Missouri. The sample of pollen from the latter had been discarded before it was realized that the amount of sterility was so much greater in 1929[2]. There is a possibility that the bud from which the pollen was taken in 1929 was parasitised by weevils or otherwise diseased. If these two plants be excepted the mean difference in sterility for eight tetraploid plants in two seasons is 3.9 percent.

The difference in the percentage sterility in hexaploids from year to year is necessarily small since they exhibit so little. Similarly, triploid plants produce so few morphologically good pollen grains that the variation in sterility shown by them in different years is slight.

OVULE STERILITY

As stated above, it has been found by several workers that morphologically perfect pollen grains are sometimes unable to function in fertilization. In his work on F_1 hybrids from *Nicotiana rusticana* × *N. paniculata*, EAST (1921) found that 2–3 percent of the pollen grains appeared to be good, but that less than 0.1 percent were functional, and that about 4 percent of the ovules were functional. He suggests that sterile female gametes are apt to coincide with the normally non-functional megaspores, and, further, that others are able to develop because they have a more favorable environment in the ovule than that to which the microspores are subjected. KRISTOFFERSON (1926) when studying interspecific hybrids in Malva found that the external nature of the pollen alone was an unreliable test

[2] In 1930 *R. polyanthema* (No. 6368) showed 42.3 percent of empty pollen grains. It is therefore probable that the low percentage figure for 1928 is in error.

for hybridity or sterility. F_1 hybrids of *Malva crispa* × *M. neglecta* showed apparently 80 percent well-formed pollen, yet this would not function when used to pollinate *M. neglecta* in a backcross. He therefore examined the number of seeds in four fruits on each plant and calculated the fertility as the ratio between the number of seeds and the number of carpels. In hybrids of *Malva neglecta* × *M. pusilla* he found that the F_1 fertility varied from 65 percent to 90 percent, and F_2 from 55 percent to 95 percent, giving, he thought, a di-hybrid segregation for sterility.

It is true for Rosa as for Fragaria (DARROW 1927) that the amount of seed set varies with the position of the flower. Therefore whenever possible the contents of terminal hips have been examined in determining ovule sterility in wild roses. It follows that the ovule sterility percentages shown in table 9 are about the minimum for each plant.

In order to determine the percentage of functional female gametes the proportion of undeveloped ovaries to the total number of ovaries in four hips was calculated. This is considered to be a measure of ovule fertility and is given in column three of table 9. Many plump achenes contain no embryos. These empty achenes can be separated out by floating in water (CROCKER 1926), those with embryos sinking after they become thoroughly wet. The proportion of the number of empty achenes (parthenocarpic fruits) to the total number of achenes gives some measure of zygotic sterility and is recorded in column two of table 9. It was interesting in this connection to find that all achenes of *R. palustris* float, a faculty which is no doubt of value to a plant which grows beside water or in bogs. The zygotic and ovule sterility is given in table 9 for fourteen wild roses selected at random. In the last column the difference between percentage ovule sterility and percentage pollen sterility is given for each individual.

The unexpected result of these few measurements is that ovule sterility appears to vary inversely with pollen sterility to some extent. The ovule sterility is larger in six plants with less than 20 percent of aborted pollen grains. The other seven native plants have over 20 percent of sterile pollen and in six of these the ovule sterility is less than the pollen sterility. In the two plants showing over 20 percent more ovule than pollen sterility, this discrepancy may be due in part to self-sterility. One of these plants is an F_1 of *R. subblanda* × *R. blanda* and the other is a vigorous hexaploid bush of *R. muriculata* Greene. There is only one plant of *R. muriculata* in our collection, and it produces many flowers but very few hips. In 1929 one bud on this plant was pollinated with *R. acicularis* Lindl. var. *Bourgeauiana* Crépin, and when ripe the hip contained a hundred plump achenes and no aborted ovules; sixty-one contained embryos. Some plants of *R.*

blanda have set more fruit in hips pollinated with *R. acicularis* than in hips which were self-pollinated.

The plants of *R. suffulta* Greene and *R. rudiuscula* Greene show about equal amounts of ovule and pollen sterility; but in a specimen of the related *R. Bushii* Rydberg there appears to have been an elimination of sterile megaspores. *R. relicta* exhibits a consistently high sterility in pollen, eggs and zygotes. The three plants of *R. blanda* examined all show a low percentage of aborted ovules together with about 50 percent of empty

TABLE 9

Percentages of ovule, zygotic and pollen sterility compared.

SPECIES AND ACCESSION NUMBER	EMBRYOLESS ACHENES (ZYGOTIC STERILITY)	ABORTED OVARIES (X) (OVULE STERILITY)	ABORTED POLLEN (Y)	DIFFERENCE BETWEEN X AND Y
R. acicularis, 6005	15	15.7	9.5	+6.2
R. muriculata, 2931	31.7	45	14	+31
R. suffulta, 2682	13.2	19.2	17.6	+1.6
" 3001	14.9	22.1	23	−0.9
R. rudiuscula, 3501	11.7	23	25.8	−2.8
R. relicta, 8320	50.9	78.6	63	+15.6
R. Bushii, 3080	27.5	9.5	25	−15.5
R. palustris, 3481		15	2	+13
R. Macounii, 3572	10.3	9.4	1	+ 8.4
R. subblanda×*R. blanda*, 11810/N7	14.5	29.1	7.5	+21.6
R. blanda, 3502/A	17.2	18.3	53	−34.7
" 3502/B	22.5	8.2	46.5	−38.3
R. blanda glandulosa, 3754/9/N8	38.8	37.3	55	−21.7
R. rubrifolia, 6394	30.9	12	(50–70)*	

* Figures given by HARRISON and BLACKBURN 1927.

microspores. Plant 3502/A produced six hips from six castrated buds in 1927 (ERLANSON 1929); buds castrated in 1929 gave no hips. Successful fruit production in *R. blanda* after castration has been observed in a few other bushes, as well as in some members of culture 3753 to which plant 9/N8 belongs. Therefore there is a possibility that the high ovule fertility in these plants of *R. blanda*, with semi-sterile pollen, may be partially due to facultative apomixis, in conjunction with the elimination of sterile megaspores. There are numbers of *R. blanda* cultures in our collection and the flowers should have been supplied with plenty of functional pollen. The two plants of culture 3502 are the only examples found so far in which the sum of the abortive ovules and empty achenes is less than the percentage of sterile pollen. The section Caninae exhibits much apomicti-

cal seed production. I have appended to table 9 the zygotic and ovule sterility found in *R. rubrifolia*, a member of this section. The pollen sterility of this individual is unknown, but HARRISON and BLACKBURN (1927) give it as 50 to 70 percent for the species. Only 12 percent of the ovules were aborted.

GENERAL DISCUSSION

It is apparent from research as to the causes of pollen and ovule sterility in plants that sterility in itself is a symptom which may be due to one or more of several causal agents. Hybridization often, though not invariably, results in a disturbance of the regularity of reduction division, and non-conjunction, lagging of chromosomes during meiosis, and polyspory appear. The same phenomena have been induced by the influence of heat and cold (STOW 1926-1927, SAKAMURA and STOW 1926, BLAKESLEE and CARTLEDGE 1927), by insect infection (KOSTOFF and KENDALL 1929), and by X-ray treatment. GOODSPEED (1929) obtained meiotic irregularities and pollen sterility, similar to those found in hybrids, by subjecting either the parental germ-cells or the pollen used to X-rays.

Triploidy, whenever it appears, causes a high degree of sterility in both male and female gametes. This is true whether the triploid plants are trivalent in synapsis and have arisen from the fusion of a diploid and a tetraploid gamete in the same species as in Datura (BLAKESLEE and CARTLEDGE 1927), Lycopersicum (LESLIE 1928), Crepis (NAVASHIN 1929) and Zea (MCCLINTOCK 1929); or whether only two sets of homologous chromosomes are present and the triploid has arisen from hybridization between different species as in Triticum (SAX 1922, THOMPSON 1926), Rubus (CRANE and DARLINGTON 1927), Nicotiana (GOODSPEED and CLAUSEN 1927, CHRISTOFF 1928) and Rosa (ERLANSON 1929). An abnormal chromosome constitution increases sterility, whether the abnormality be the presence of one or more extra chromosomes (BLAKESLEE and CARTLEDGE 1927, LESLIE 1928, MCCLINTOCK 1929) or a deficiency (HUSKINS 1927, 1928).

There are also genes responsible for sterility, as the "bad pollen inducers" in Datura (BLAKESLEE and CARTLEDGE 1927). These factors segregate in F_2. SALAMAN (1910) found that in the potato male sterility is a dominant Mendelian character. A curious inheritance of semi-sterility in descendants from a cross between two species of Stizolobium was described by BELLING (1914). The F_1 plants had 50 percent of both male and female gametes non-viable. Half of the F_2 progeny resembled the F_1 hybrids in the semi-sterility of their gametes, the rest had perfect pollen and good ovules and gave fully fertile offspring. The pollen in wild forms of

Mentzelia intermediate between *M. multiflora* and *M. nuda* was found by CLEMENTS and PENLAND (1926-1927) to vary from 5 percent to 95 percent sterile. This shows that segregation of sterility types occurs in nature. The wide variation in pollen sterility found by the writer in most diploid and tetraploid North American wild roses suggests that genetic factors are at least partially responsible.

The percentages of defective pollen grains found in Vitis by DORSEY (1914) reveal a considerable range in variation for *Vitis vulpina* (from 0 percent to 45 percent), though the sterility is under 5 percent for both male and female vines. Cultivated varieties exhibited an average of about 23 percent of defective pollen, whether they were of hybrid origin or not. DORSEY concludes that in this genus pollen sterility is not necessarily caused by hybridization, but may be a step towards functional dicliny.

The effect of polyploidy upon sterility is not always the same. DARLINGTON (1928) pointed out that there seems to be an inverse correlation between the sterility of a diploid and the fertility of a tetraploid to which it gives rise. JØRGENSON (1928) by inducing somatic doubling in diploids obtained tetraploid Solana which were less fertile than the diploids. The pollen of tetraploid plants of Datura is less fertile than that of diploids (BLAKESLEE and CARTLEDGE 1927). LONGLEY (1927) found that tetraploid Rubus forms, both wild and cultivated, had a greater percentage of pollen sterility than the diploid forms, while the higher polyploids were less sterile. Many instances are now known of the production of a fertile tetraploid from a sterile diploid hybrid and the literature has been reviewed often. MEURMAN (1929) found that in *Prunus laurocerasus* the basic chromosome number for the genus was present about 22 times, and that in such a high polyploid tetrad formation and viability of gametes are unaffected by the lagging of some of the chromosomes. The pollen in diploid, tetraploid and hexaploid species of Triticum is equally fertile, but pentaploid hybrids are less sterile than triploid hybrids (SAX 1922). Similarly LONGLEY (1927) gives figures showing that pentaploid forms in Rubus have slightly less poor pollen than the triploids.

In the American roses of the Cinnamoueae the mean pollen sterility is about the same in related diploid and tetraploid species. There are, however, some tetraploid plants which show a very high degree of sterility. These latter may have originated from an unreduced egg in a diploid, fertilized by pollen from a tetraploid. A tetraploid Rubus obtained in this way in the F_1 progeny of *Rubus rusticanus inermis* × *R. thyrsiger* was highly fertile (CRANE and DARLINGTON 1927), but it is conceivable that sometimes maturation in such a tetraploid would be irregular.

In considering female fertility in plants we are forced usually to deal with zygotic fertility, since it is often impossible to obtain large numbers of megaspores or even of embryo-sacs for statistical studies. Female fertility is affected by the factors enumerated above as affecting pollen sterility, and further by self-sterility, by apomixis and by purely environmental conditions affecting the nourishment of the fruit, such as unsuitable soil (SCHUSTER 1926). Many sterile megaspores are no doubt eliminated after meiosis among those that normally develop no further. If the pollen is highly sterile some normal embryo-sacs may fail to develop owing to lack of sufficient functional microspores, as found in wheat hybrids by WATKINS (1925).

Self-sterility, another important factor in causing reduced seed production, is particularly widespread in the family Rosaceae (SUTTON 1918, CRANE 1925). It is undoubtedly present to some degree in some wild roses. This again is a manifestation of many complex genetic and physiological factors (EAST and MANGELSDORF 1925).

Since some roses are facultatively apomictical, a plant may be judged more fertile than is actually the case, if seed production be taken as a criterion.

CONCLUSION

GOODSPEED (1929) has recently pointed out that the successful production of fertile gametes in plants depends upon nicely balanced physiological growth factors arranged in a particular manner in the living organism. This balance can be upset by a number of agents, environmental, physiological, or hereditary. Hybridity is only one of these agents and its effect is conditioned by the compatibility of the parents.

HURST'S contention (HURST 1925, 1928) that either fertile or sterile offspring will result from hybridization between diploid rose forms is not borne out by the analysis of the pollen in the few F_1 hybrids thus far obtained by the writer. There is a wide variation in the amount of pollen sterility in most cultures of rose species. Sterile pollen up to 25 percent appears to be characteristic of relatively fertile plants in any species and may be due to conditions affecting growth and nutrition of the pollen mother cells.

It is probable that a wild rose plant with over 70 percent of the pollen grains aborted, and which sets little or no fruit, is an F_1 hybrid. Partially sterile plants and even those showing a relatively high production of good pollen may also be hybrids. There is only one way by which we may come to know much about the amount of hybridization among roses in nature,

and that is to grow large progenies of seedlings from single wild seed parents, and to make interspecific crosses artificially. I do not believe that it is possible to predict what the result will be in any species cross owing to the high degree of heterozygosis and consequent variation within each species. Dependence upon the degree of sterility alone as sufficient evidence for or against hybridity is unwarranted by the facts that have been assembled.

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FRONTISPIECE

Professor Doctor ERWIN BAUR, Ph.D., M.D., D. Agr. (h.c.), Director of the INSTITUT FÜR VERERBUNGSFORSCHUNG in Berlin-Dahlem, and of the INSTITUT FÜR ZÜCHTUNGSFORSCHUNG recently erected by the Kaiser WILHELM GESELLSCHAFT at Müncheberg near Berlin, was born at Ichenheim, Baden, April 16, 1875, and educated at the universities of Heidelberg, Freiburg, Strassburg and Kiel. He passed the state examination in medicine at Kiel in 1900 and was for a short time a practicing physician. In 1904 he became Privatdozent in Botany in the UNIVERSITY OF BERLIN, and in 1910 Associate Professor of Botany in the same institution. In 1911 he was called to a full Professorship and made Director of the Botanical Institute of the LANDWIRTSCHAFTLICHE HOCHSCHULE in Berlin, in succession to Professor Doctor L. KNY. In 1913 he was made Professor of Genetics in the same institution and a special institution was erected for him, first provisionally at Potsdam, but in 1921 the present institution was erected under his guidance at Berlin-Dahlem. He founded the *Zeitschrift für induktive Abstammungs- und Vererbungslehre*, *Bibliotheca Genetica*, and *Der Züchter;* and is Associate Editor of *Zeitschrift für Pflanzenzüchtung*, *Fortschritte der Biologie*, and *Gartenbauwissenschaft*. As Chairman of the Organization Committee he presided at the opening of the Fifth International Genetical Congress in Berlin in 1927. In 1914 he was chosen as Exchange Professor at the UNIVERSITY OF WISCONSIN but was prevented by the outbreak of the war from filling this mission.

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